Responses of rodent populations to spatial heterogeneity and successional changes within Sitka spruce (Picea sitchensis) plantations at Hamsterley Forest, County Durham.

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RESPONSES OF RODENT POPULATIONS TO SPATIAL HETEROGENEITY AND SUCCESSIONAL CHANGES WITHIN SITKA SPRUCE (*Picea sitchensis*) PLANTATIONS AT HAMSTERLEY FOREST, COUNTY DURHAM

by

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To my father, to my mother, and to my Rodentia.

"Mice are merely the protusion into our own dimension of vastly hyper-intelligent, pandimensional beings. The whole business with the squeaking and the cheese is just a front"

Douglas Adams, "The Hitchhiker's Guide to the Galaxy"

ABSTRACT - Responses of rodent populations to spatial heterogeneity and successional changes within Sitka spruce (*Picea sitchensis*) plantations at Hamsterley Forest, County Durham. Populations of woodmice (*Apodemus sylvaticus*), bank voles (*Clethrionomys glareolus*) and field voles (*Microtus agrestis*) were studied by live-trapping in Sitka spruce plantations at Hamsterley Forest, northeast England, from February 1990 to June 1992. The study was carried out at two distinct spatial scales.

At the coarser spatial scale, the effects of successional change and of spatial (inter-site) heterogeneity within the forest were compared by censusing rodent commmunities in sites representing three successional stages: mature plantations (about 40 years after planting), clear-fellings and young plantations (5-8 years after planting). In mature plantations woodmice and bank voles were both abundant, in clear-fellings the former were usually dominant and in young plantations field voles were also abundant alongside the other two species. Pooling all sites, in young plantations rodent communities had highest diversity and evenness, mostly because of an inter-site component (β-diversity). On a site-by-site basis, in young plantations communities had neither higher α-diversity nor evenness than in mature plantations. Clear-fellings showed least diversity and evenness. Multivariate analyses revealed marked taxonomic and structural changes in vegetation during succession and how the rodents responded to such changes. Within young plantations bank voles were associated with dense ground cover, provided mostly by heather. Field voles were associated with the non-palatable grass *Deschampsia flexuosa* and to palatable grasses as well. Woodmice were habitat generalists, but their abundance was negatively correlated with that of field voles. Spatial heterogeneity in soils explained much of the inter-site variation in ground vegetation which in turn explained much of the β-diversity in rodent communities in young plantations.

At the finer spatial scale, populations of woodmice and bank voles were studied by monthly trapping in five 0.81 ha grids within an habitat mosaic produced by the felling of a plantation of mature Sitka spruce. Inter-grid movements were frequent for both species, but especially woodmice, which also had larger home ranges. Population dynamics of woodmice in the whole mosaic were apparently similar to patterns described previously in other habitats, except that density-dependent reduction of survival and reproduction by late autumn was more severe than usual. Woodmice were more abundant in 1991 than in 1990, apparently due to increased seed supply. Bank voles, in contrast, did not show regular annual fluctuations in numbers. Although breeding stopped in both winters, population densities increased steadly during 1991 and remained high until spring 1992. Clear-felling of a part of the study area had little immediate effect on populations of either species; responses to clear-felling were gradual rather than sudden. The experimental removal of tree brashings from recent clear-fellings scarcely affected the populations of woodmice, but made the clear-fellings unsuitable for bank voles, apparently due to the reduced availability of shelter. Habitat selection within the whole habitat mosaic was density-independent in bank voles, but density-dependent in woodmice. In the later species, demographic differences among local subpopulations accounted for most of the observed density-dependent changes in spatial distribution, although inter-grid movements also played an important part.

The responses of each rodent species to spatial and temporal heterogeneity and a possible role of density-dependent habitat selection in population regulation are discussed.

I certify that all material in this thesis which is not my own work has been identified and that no material is included for which a degree has previously been conferred upon me.

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CHAPTER 1
INTRODUCTION

This thesis presents the results of my research into the responses of small rodent populations to changes in time and space in the structure of a planted conifer forest. The present Chapter aims to insert my study in the context of previous studies on related topics, to briefly introduce the biology of the main species involved, and to present the structure of the rest of the thesis.

1.1 - Habitat fragmentation, spatial and temporal habitat heterogeneity, and small mammal populations - The process of habitat fragmentation is one of the greatest changes that man has caused to the biological world in modern times. Many natural habitats which were essentially continuous a few generations ago have been reduced to a mosaic-like landscape formed by scattered "patches" of the original habitat ("habitat islands") surrounded by transformed areas. A few detailed examples of the process of fragmentation are described in Shafer, 1990, but other examples are increasingly easy to find. Intense habitat fragmentation is already characteristic of nearly all developed countries, and the same process is now well under way in most tropical regions (Harris, 1984). Using Hutchinson's (1965) metaphor, the evolutionary play is now staged in a markedly different ecological theatre.

In addition to spatial heterogeneity between the original and transformed habitats, the process of habitat fragmentation often tends to increase temporal heterogeneity as well. One of the main sources of temporal heterogenity is succession: in many cases the original continuous habitat was the local climax vegetation, which is partly replaced by earlier successional stages which are usually more unstable. Often such successions are actually blocked in early stages (for example, where forest gives way to pastureland), but if allowed to proceed they result in successional habitat mosaics, patchworks where different habitat patches correspond to different successional stages of the same community. Additionally, isolated habitat patches of small area can be very unstable and prone to further changes, even in the absence of additional human disturbance. This was dramatically shown in small isolates of tropical forest in Amazonia, where the trees along the edges are very vulnerable to windthrow, so that isolation itself virtually condemns the forest relicts to additional changes (Lovejoy *et al.*, 1986). In cases where human influences have increased both spatial and temporal habitat heterogeneity, landscapes have

often evolved into complex "shifting habitat mosaics", patchworks of habitats transformed in many different ways and changing continually in time.

Understanding the effects of habitat fragmentation on biological communities is essential as a basis for sound wildlife conservation and management practices in the modern world (Harris, 1984; Shafer, 1990). As mammals in general have relatively large body sizes, low population densities, and less vagility than birds, for example, mammal communities are objects of special concern for conservation. If areas surrounding preserved patches are unsuitable for some species, as is often the case, then from the point of view of those species the habitat patches constitute true "islands" in a biogeographical sense. In such islands the diversity of the mammal communities is likely to be reduced by the combined effects of reduced area - which increases extinction rates of the original species - and increased isolation - which reduces rates of colonization by new species and also the genetic viability of the populations within the "island" (MacArthur and Wilson, 1967; Brown and Kodric-Brown, 1977; Gilpin and Soule', 1986; Shafer, 1990).

Large sized mammals are considerably more vulnerable to extinction by habitat fragmentation than small ones, because of smaller population sizes which increase the probability of extinction by either demographic stochasticity or loss of genetic variability due to inbreeding (Gilpin and Soule', 1986). Thus most reduction of diversity in fragmented mammal communities is effected by extirpation of the largest species, and/or the ones of highest trophic level such as carnivores (Wilcox, 1980). However, habitat fragmentation, and in particular "shifting habitat mosaics" as defined above, are also likely to have several important effects on populations of small mammal species (i.e. rodents and insectivores around most of the World, and marsupials in Australia and in the Neotropical Region).

Study of the effects of spatial heterogeneity on small mammal populations has been a focus of considerable recent research. One of the first reasons for this interest was theoretical: the realization that spatial heterogeneity could be important for regulating non-cyclical populations of microtine rodents (voles and lemmings) in Fennoscandia (e.g. Hansson, 1977; Stenseth, 1977, 1980, 1985; Hestbeck, 1982). More recently, conservation aspects of habitat fragmentation have been emphasized in studies in a variety of tropical and subtropical biotas around the world. For example, Bennett (1990) studied the importance of habitat corridors for the conservation of marsupial and rodent populations in a fragmented *Eucalyptus* forest in Australia, and Fonseca and Robinson (1990) compared the small mammal communities in patches with and without mammalian predators within the Brazilian Atlantic Forest. In Europe, where habitat fragmentation is widespread, many studies have been carried out on responses to spatial heterogeneity of

populations of the commonest woodland rodents (woodmice, *Apodemus* spp., and bank voles, *Clethrionomys glareolus*). Several of the recent studies have focused on population dynamics in isolated patches and movements between patches in different types of habitat mosaics. Cases studied included fragmented woodlands in Belgium (Geuse *et al.* 1985, Bauchau and Le Boulengé 1991), urban habitats in Oxford (Dickman and Doncaster, 1987, 1989) and in Warsaw (Szacki and Liro, 1991), and an agricultural landscape in Yorkshire (Zhang and Usher, 1991). The responses of these species and field voles (*Microtus agrestis*) to temporal habitat variation, especially succession, have also been analysed in several localities in Britain and continental Europe (as reviewed in Chapter 3 of the present study).

Few studies so far have considered simultaneously the effects of spatial and temporal habitat heterogeneity on the most common British rodents. Flowerdew *et al.* (1977) studied habitat preferences of four rodent species in a fenland habitat mosaic subject to flooding in East Anglia, and Montgomery *et al.* (1991) studied how local and interannual differences in seed availability affected the distribution of *A. sylvaticus* within a forest (mostly coniferous) in Northern Ireland. The present study addresses the effects of spatial heterogeneity and successional changes on rodent populations in a planted coniferous forest in northeast England.

1.2 - Planted forests as a model for studies on small mammals in shifting habitat mosaics - Man-made forests can be especially suitable for studying the effects of spatial and temporal heterogeneity on small mammal populations and communities, for several interconnected reasons, as follows.

Planted forests, especially commercial ones, are often dominated by one or a few tree species, so that the mature plantations constitute a single, well-defined "climax" community. As mature plantations are felled and replaced by younger ones, over large forest areas a typical successional habitat mosaic is formed, with different patches corresponding to older plantations, younger plantations, clear-fellings, and so on. This successional habitat mosaic resembles situations found in natural mono-species conifer forests in the taiga belt in Northern Europe. A major difference could be the clear-felling of some patches of mature forest at chosen times in planted forests. However, the role of clear-fellings in restarting succession in a few patches at a time is parallelled by wind-throws in natural conifer forests, with the difference that the fallen trees stay in the wind-throws, while the trunks are removed in clear-fellings (although pieces of no commercial value are often left *in situ*). Another difference between planted and natural forests is that in the former the boundaries between the successional patches are sharply defined (by the

limits of each plantation "compartment") and the successional stage of each patch can be unambiguously assigned.

This mosaic of sharply distinct patches provides good opportunities to study small mammal population dynamics and spatial distributions in heterogeneous habitats. Additionally, the well-defined successional habitat mosaics of planted forests are suitable for study of the effects of succession on the mammals by simultaneously sampling sites of different stages, without need to follow the long trajectory of succession in a single place (the so-called chronosequence approach; Twigg *et al.*, 1989, Fox, 1990).

However, local variation in species composition and relative abundance in small mammal communities within a single vegetation type is often very marked (e.g. Brown and Kurzius, 1989) and successional stage alone is unlikely to explain all the variation between different patches. In a monospecies forest one important variable (the dominant tree species) is held constant in all sites. This makes it easier to compare the effects of temporal (successional) change with those of spatial heterogeneity as reflected in local variation among different sites representing the same successional stage.

As a whole, planted forests can be seen as simple models in which the effects of spatial and temporal heterogeneity on small mammal populations and communities can be studied, where techniques and ideas can be developed for later application in more complex natural forests, either in the temperate or in tropical regions.

Besides providing a good model system, planted forests merit considerable attention because of the vast areas they cover in the landscape today in both the developed and developing countries around the World. In Britain, large areas have been planted with conifer trees since the early 1920's, following the setting up of the Forestry Commission in 1919 (Rowan, 1986). Today conifers account for more than two thirds of British woodland, covering over 1.3 million hectares out of nearly 1.9 million hectares of high forest; approximately 80% of the former area refers to plantations of introduced conifer species (Petty and Avery, 1990).

Many of the early large scale Forestry Comminssion plantations have become mature and ready for felling during the last two decades. Thus, an important change is happening over large areas of the British coniferous forests (Rowan, 1986), namely the start of the second rotation, the replanting of conifers on sites previously occupied by similar plantations. An important difference between first and second rotation plantations is the presence in the latter of piles of tree brashings, branches and pieces of trees without commercial value which often are left *in situ* when the trees are removed after felling. Among other effects, tree brashings may hinder the colonization of the young second rotation plantations by some plant species. As the tree brashings are gradually

decomposed, the difference between first and second rotation should become smaller in mature than in young plantations. On the other hand, little is known as to whether plantations of successive conifer rotations in Britain will be affected by cumulative effects of the trees on soils (Miles, 1986). Due to the recent introduction of second rotation in Britain, there are few studies on rodent populations in British second rotation conifer plantations (as reviewed by Staines, 1986), although a series of recent studies (e.g. Thomson, 1986; Gibson, 1989; Vadher, 1990) are starting to fill this gap.

1.3 - Sitka spruce in Britain - Sitka spruce (*Picea sitchensis* Carriere), the main tree species involved in the present study, is a native of the western coast of North America, where its original range lies between California and Alaska (Faulkner and Wood, 1957). First introduced to Britain in 1831, *P. sitchensis* is now the most abundant tree species in the Britain Isles: it alone accounts for over half a million hectares of British woodland, i.e., nearly as much as all broadleaved species put together (Petty and Avery, 1990). Sitka spruce in its native range is one of the tallest of all living trees, as individuals several hundred years old may reach up to 90 m in British Columbia (Chiras, 1990). However, in short-rotation commercial plantations this species is felled when 50 years old or less, long before it reaches its maximum size. Thus British "mature" Sitka spruce plantations are actually forests of young trees, but throughout the present study I use the word "mature" Sitka in its forestry meaning, i.e., old enough to be suitable for felling.

The native distribution of Sitka suggests that it has a high moisture requirement. That was no barrier for the establishment of the species in most places in Britain, where it soon acquired a good reputation because of its rapid rate of growth, high volume of production, straight trunks, ease of establishment even in relatively poor soils, and a considerable tolerance to exposure (Faulkner and Wood, 1957). Such qualities, shown in the earlier plantations, encouraged further planting of Sitka, which in the last few decades has accounted for a progressively larger proportion of the conifers planted in Britain (Rowan, 1986). However, Sitka's early success led to an underestimation of some of the problems it encountered on poorer soils such as the least fertile peats, and when planted in sites where heather (*Calluna* spp.) is present. In the absence of grazing heather may become dominant and Sitka grows slowly, if at all; sometimes pine has to be planted with Sitka to help in suppression of heather (Faulkner and Wood, 1957).

Although Sitka seeds begin to be shed by October of the year in which they are produced (Brown and Neustein, 1972, quoted in Hill, 1986), a considerable proportion is retained overwinter in the cones at the top of the trees and are dispersed only in the following year, starting in spring (B. Walker, Forestry Commisssion, pers. comm.).

Therefore the number of seeds dispersed in a given year is correlated with the seed production from the previous year.

Sitka spruce is an especially interesting model species for study of the effects of temporal heterogeneity on small mammal populations, because successional changes in plantations of *P. sitchensis* are especially quick and clear-cut. Mature Sitka spruce trees develop very dense branches which block the passage of light, especially in the commercial plantations where tree densities are usually higher than in natural forests. In mature Sitka spruce plantations little light reaches the forest floor and consequently the ground is completely bare, except for mosses; all other vegetation is shadowed out (Hill, 1979). Although this trend is reversed later in natural spruce forests (where senescence of trees eventually makes the canopy slightly more open and ground vegetation can invade), commercial spruce plantations are harvested before senescence starts, thus ground vegetation is largely absent by the time the forest is clear-felled. After clear-felling ground vegetation starts to colonize the young plantations. Typically, from some five years after planting a rich ground layer of grasses, heather, bramble, bracken, rushes and herbs is found amidst the small conifer trees (Gibson, 1989). This is a completely different habitat for rodents from the mature forest found in the same sites a few years before. However, this habitat is short-lived, as the canopy starts to close when the plantations are about fifteen years old. In other species of conifers this stage of succession can induce dramatic changes in rodent communities over a period of a few years (Ferns, 1979a). Due to Sitka's rapid growth, all the marked habitat changes in the successional cycle take place within forty to fifty years, i.e. the lenght of a rotation.

As compared to broadleaved trees, the litter from Sitka spruce and other conifers decomposes slower. Litter under broadleaved stands tends to be transformed quickly by soil macro-decomposers into small particles which are readly mixed with the mineral horizons of the soil (as "mull" humus) where it continues to decay. Conifer litter in contrast tends to lie on the soil surface for many years (as "mor" humus), being slowly degraded by microbial decomposers before soil animals are able to transform it into small particles which can mix with the soil; one reason for this is that conifer litter tends to be more acid and to have a higher tannin content, which makes it less palatable to earthworms and other animal decomposers (Satchell, 1967, quoted in Miles, 1986). As consequences of this difference in decomposition, conifers in general, when growing on soils susceptible to rapid change, tend to promote more surface acumulation of organic matter, greater acidity, and a higher degree of soil podzolization than broadleaved species (review in Miles, 1986). Podzols are well-drained, very acidic soils which are characterized by an intermediate horizon which is nutrient-poor due to leaching (Avery,

1990). Norway spruce (*Picea abies*) has been widely studied in continental Europe where reports from at least ten countries show that it reduces soil pH and causes or accelerates podzolization; although less well studied, the congeneric species, Sitka spruce, apparently shows similar effects in Britain (Miles, 1986). The rate of change in pH and in the speed of the process of podzolization can vary greatly from site to site, according to the local characteristics of the soil. Well-drained, poorly buffered soils are most vulnerable to change; conversely, water-logged, well buffered soils are quite resistant to changes in pH and to podzolization (Miles, 1986).

1.4 - The ecology of woodmice, bank voles and field voles: some contrasts - The small mammals involved in the present study are the three most common British wild rodents, i.e., the wood mouse (*Apodemus sylvaticus* L.), the bank vole (*Clethrionomys glareolus* Schreber) and the field vole (*Microtus agrestis* L.). The three species are widely distributed through Europe and their ecology has been extensively studied in Britain and elsewhere, as reviewed by Flowerdew (1984, 1991), Flowerdew *et al.* (1985), Alibhai and Gipps (1991) and Gipps and Alibhai (1991). In the present Section I use some findings of previous studies to position the three species along continua defining possible strategies of feeding, movements and habitat preferences. I am aware that this scheme is a simplification for two reasons: first because linear continua are an artificial way of representing ranges of possible strategies, and second because within each species there is seasonal and/or geographical variation in several of the parameters described below. However, I suggest that in each case there is a recognizable order in which the three species can be arranged along the possible range of strategies, and that these orders are relevant to an understanding of the different responses of these rodents to spatial and temporal habitat heterogeneity.

1) Feeding strategies - Woodmice are mostly seed eaters, and among the three species they eat the largest proportion of animal food; bank voles eat a wider variety of plant foods such as seeds, berries, roots, leaves and fungi, but less animal food; field voles are mostly grass specialists and seldom eat any animal food (Watts, 1968; Evans, 1973; Ferns, 1976; Obrtel and Holisova, 1979; Hansson, 1985; Montgomery and Montgomery, 1990; Zubaid and Gorman, 1991). As pointed out by Holisova and Obrtel (1980), these differences define a gradient of feeding strategies: woodmice usually concentrate on high quality, sparsely distributed food, bank voles are intermediate, and field voles depend on abundant food of low energetic value.

2) Home ranges and extent of movements - Woodmice are highly vagile animals, using a large home range for an animal of its size and making long dispersal movements; bank

voles have home ranges of intermediate size, and field voles have very small home ranges and restricted movements (e.g. Brown, 1966, Watts, 1970, Wolton and Flowerdew, 1985, Attuquayefio *et al.*, 1986, Gipps and Alibhai, 1991). This pattern is apparently related to the differences in feeding strategies discussed in the previous paragraph: the species which uses the most densely distributed food has the smallest home range, and vice-versa.

3) Degree of habitat specialization - Woodmice are highly adaptable, being common in a wide variety of habitats; bank voles also use several habitats but are more restricted by their dependence on ground cover; field voles are the most habitat specialist of the three, living mostly in rough grassland and young forestry plantations with a lush growth of grass and seldom being found in appreciable densities in other habitats (Southern and Lowe, 1968, Gurnell, 1985, Flowerdew, 1991, Alibahi and Gipps, 1991, Gipps and Alibhai, 1991). The ubiquitous distribution of woodmice apparently is related to their generalist diet, plus strategies of predator avoidance that depend chiefly on nocturnal habits, agility and use of burrowing systems; the voles which are partly diurnal depend more on ground cover (Brown, 1956a; King, 1985).

1.5 - Thesis structure - This thesis is organized in seven chapters, starting with a general Introduction (present Chapter). Chapter 2 describes the study area, Hamsterley Forest, and discusses methodological aspects which are common to all parts of the study. There follow four semi-independent chapters (3 to 6), which are the core of the thesis. Each of these chapters has its own Introduction, Methods, Results and Discussion sections. The specific goals of the part of the study described in each Chapter are stated in the respective Introductions. Conceptual and/or theoretical aspects which are relevant specifically to each Chapter are reviewed in their respective Introduction sections, or in their Discussion sections if this was more suitable (e.g., previous studies on population dynamics of woodmice and bank voles are briefly reviewed in the Discussion of Chapter 4 to allow comparisons with my own results). My results are presented in Chapters 3 to 6, and most discussion of their implications is carried out in the respective Discussion sections. The contents of these chapters are briefly outlined below.

Chapter 3 discusses the variation in species composition and relative abundance of rodent communities in relation to successional change and to spatial heterogeneity in Sitka spruce plantations in Hamsterley Forest. The overall pattern of variation in rodent community composition with succession is characterized. In young plantations, the successional stage in which maximum heterogeneity was found among different sites, the relative abundances of rodent species are related to local vegetation composition and structure and to soil characteristics. This Chapter describes a study on a larger

geographical scale (the forest as a whole) than the remaining chapters; it is also the only Chapter in which rodents are studied chiefly with a community, rather than population, approach.

Chapter 4 discusses the population dynamics of woodmice and bank voles in a shifting habitat mosaic formed by mature plantations and clear-fellings. This Chapter, as well as the two following ones, deals with a smaller spatial scale than Chapter 3: population processes are studied in an area within and around a single compartment of the forest (the so-called Corner Complex). As rodent individuals often are not restricted to single sites within this mosaic, Chapter 4 discusses rodent population dynamics in Corner Complex as a whole. My results are compared with previous studies on population dynamics of the two rodent species in other habitats.

Chapter 5 describes the responses of woodmice and bank vole populations to clear-felling of a mature plantation within Corner Complex. It discusses how that drastic habitat change influences the distribution of rodents among subareas within the area studied in Chapter 4. For this purpose two field experiments were used: first, the "natural" field experiment represented by the felling itself; second, the removal of tree brashings on recent clear-fellings to evaluate the importance of shelter in such habitats for each rodent species.

Chapter 6 focuses on density-dependence in habitat selection: it relates the variations in rodent population densities to how widely they are distributed within the habitats mosaic of Corner Complex. The different patterns shown by woodmice and bank voles are contrasted, and two methods to study density-dependent habitat selection are discussed. This Chapter also analyses how important are movements between sites in promotion of changes in spatial distribution associated with changes in density of woodmice.

The final Chapter (seven) is a general Discussion which connects the results of the previous Chapters. It compares the species of rodents regarding their responses to spatial and temporal heterogeneity, discusses how the planting of Sitka may influence spatial heterogeneity within the forest, and suggests a hypothesis relating the differential responses of rodent populations to spatial heterogeneity with their distinct patterns of fluctuations in numbers.

CHAPTER 2
STUDY AREA AND GENERAL METHODS

2.1 - Hamsterley Forest

Hamsterley Forest, owned and managed by the Forestry Commission, is located in the southwest part of County Durham (longitude 01° 55' W, latitude 54° 39' N), approximately 40 Km to the South of the City of Durham. It lays on the eastern side of the Pennines, between the rivers Tees and Wear. The forest itself covers a total area of 2,020 ha, emcompassing the catchment area of a tributary of the river Wear, Bedburn Beck, plus Bedburn Beck's own major tributary, Euden Beck. The lowest point in the forest (at Bedburn, in the east) lies at approximately 150 m and the land rises to the west, reaching a maximum altitude of 430 m (Gibson, 1989). The underlying geology of the area is sand and mudstone of the millstone grit era (Malvido, 1989). The predominant soil type is peaty gley, but there is considerable local variation in soil types within the forest, discussed in Chapter 3.

The area where Hamsterley Forest lies today was a shooting estate and grouse moor before being purchased by the Forestry Commission in 1927. Planting of the first rotation took place from the late 1920's until 1951. During these early decades of the Forestry Commission, several different conifer species (most imported) were test-planted, which explains why a high number of different conifer species is found now in Hamsterley. In 1989, 86% of Hamsterley Forest was covered by conifer plantations, 8% by pastures, recreation areas and roads and 4% by broadleaved woodland (Walker, 1989, quoted in Vadher, 1990). A farm (Pennington Farm) is located within the forest and the recreation areas are mostly managed grasslands used for camping and picnics. The areas surrounding the forest are covered mostly by rough pasture, moorland and agricultural fields.

Within the forest, Sitka spruce (*Picea sitchensis*) is the commonest tree species. In 1989 it alone covered 880 ha - approximately 51.5 % of the total area of conifers. The second most common tree in Hamsterley is the native conifer Scots pine (*Pinus sylvestris*). The remaining conifer species, covering relatively small areas within the forest, include Douglas fir (*Pseudotsuga menziesii*), Norway spruce (*Picea abies*), European larch (*Larix decidua*), Japanese larch (*L. leptolepis*) and Western hemlock (*Tsuga heterophylla*). The relatively small area of deciduous woodland consists mostly of a few blocks of oak (*Quercus robur*) and trees planted along streamsides and roadsides, especially oak, birch

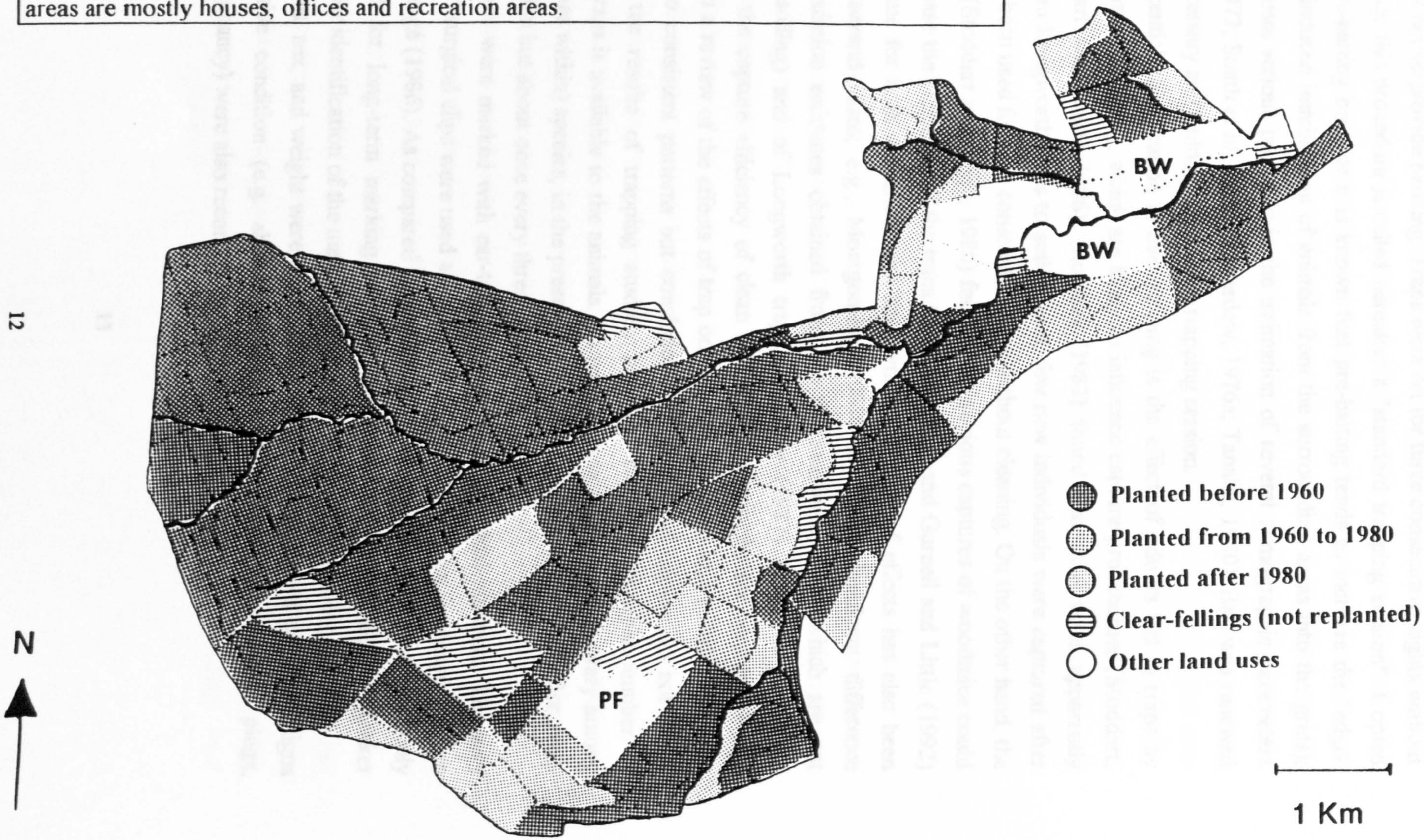
(*Betula pendula*), beech (*Fagus sylvatica*) and sycamore (*Acer pseudoplatanus*). Due to the commercial advantages offered by Sitka spruce, the predominance of this species has increased steadily in Hamsterley during the last few decades, as has happened in Forestry Commission plantations in general (Chapter 1). Nearly all conifers planted in Hamsterley from 1980 to the present day have been either predominantly or entirely Sitka spruce.

By the start of the present study in early 1990, most conifer plantations in Hamsterley were reaching the end of the first rotation (i.e. they were about 40 years old or more), but comparatively few sites had already been felled and replanted. Figure 2.1, based on Forestry Commission timber extraction maps on the scale of 1:10,000, shows the distribution of conifer plantations of different ages and of clear-fellings within Hamsterley Forest in February 1990. Mature plantations predominated over younger plantations (i.e. the two categories "planted from 1960 to 1980" and "planted after 1980" in Figure 2.1) in the habitat mosaic in Hamsterley at that time. Some of the recent clear-fellings, including all those sites described in the following Chapters, were left to natural regeneration and not replanted within the duration of the study.

2.2 - Capture - mark - recapture methods

2.2.1 - Trapping and marking techniques - Within each site chosen for study a square grid of 49 points (7 x 7) was marked, using a hand compass and metric tape. The spacing between points was 15 m, thus the area delimited by each grid was 0.81 ha. Points were marked with bamboo canes, except in the mature forest grids where plastic yellow tape attached to the trees was found to be preferable to canes. The shape and size of these grids were similar to those used in the Mammal Society Woodland Small Mammal Survey coordinated by J.R. Flowerdew. Unlike the Survey grids, in my grid design only one trap was placed at each point. I opted for using one trap per point as a compromise between my ability to operate the grids in times of high catches and the need to trap in several sites simultaneously, but arguably having only one trap available in each point might lead to competition for traps among the rodents and consequent failure to catch a part of the population. However, according to Southern (1973), reasonably consistent estimates of rodent population sizes will be produced if at least 20% of the traps are unoccupied in every trapping night. During my study this condition failed to be fulfilled in one occasion only (grid Corner 2 in October 1991; see Chapters 5 and 6). Thus it is likely that competition for the traps did not seriously affect the population size estimates in most occasions. The design I used is referred to hereafter as the "standard grid".

FIGURE 2.1. The habitat mosaic within Hamsterley Forest: distribution of conifer plantations of different ages and clear-fellings in 1990. Areas subject to other land uses are also shown (blanks), including Pennington Farm (PF) and broadleaved woodland (BW); remaining blank areas are mostly houses, offices and recreation areas.



Live-trapping was performed using Longworth traps (Chitty and Kempson, 1949; Gurnell and Flowerdew, 1982) baited with a few grams of whole wheat and crushed oats, and filled with hay to provide bedding. Traps were set for three consecutive nights without any pre-baiting; this procedure is called hereafter a "standard trapping session". I opted not to use pre-baiting because it is known that pre-baiting tends to increase the "edge-effect" (trap-induced immigration of animals from the surrounding areas into the grids); this effect causes serious problems in the estimation of several demographic parameters (Southern, 1973; Smith *et al*, 1975; Flowerdew, 1976a; Tanaka, 1980). Bait was renewed whenever necessary and bedding after every trapping session.

A potential complication in live trapping is the effect of odours left in traps by animals captured previously, which are likely to influence capture probabilities (Stoddart, 1982; Stoddart and Smith, 1986). Stoddart (1982) found that field voles apparently preferred clean Longworth traps to soiled ones; few new individuals were captured after the traps had been used for nine consecutive days without cleaning. On the other hand, the same author (Stoddart and Smith, 1986) found that previous captures of woodmice could actually increase the efficiency of the traps for conspecifics and Gurnell and Little (1992) found the same for both woodmice and bank voles. Absence of effects has also been reported in several cases; e.g., Montgomery (1987) found no significant difference between population estimates obtained from use of breakback traps (which are not affected by soiling) and of Longworth traps, and Tew (1987) found no detectable difference in the capture efficiency of clean and dirty Longworths for bank voles and woodmice. In a review of the effects of trap odours, Gurnell and Little (1992: table VII) could find no consistent patterns but concluded that in general odours do not affect significantly the results of trapping studies, provided that a reasonable number of unoccupied traps is available to the animals. As responses to odours seem to vary among (and sometimes within) species, in the present study the traps were not washed after every trapping session but about once every three sessions.

Rodents were marked with ear-tags stamped with individual numbers. The very light "Michel" surgical clips were used as ear-tags, as introduced by Le Boulengé-Nguyen and Le Boulengé (1986). As compared to toe-clipping, which is the other most commonly used method for long-term marking of small mammals, ear-tagging allows quicker marking, easier identification of the mark, and less suffering to the animals.

Species, sex, and weight were recorded for all individual rodents captured. Signs of reproductive condition (e.g. abdominal testes, perforate vaginas, vaginal plugs, lactation, pregnancy) were also recorded whenever observed.

2.2.2 - Dealing with tag losses - Loss of a Michel tag can be recognised easily from a characteristic tear left in the skin of the ear. During the study I detected a rate of tag loss of 6.4% for woodmice, 6.0% for bank voles and zero for field voles (but only 16 recaptures were obtained for this species). Rates of tag loss for woodmice and bank voles are slightly higher than the ones reported by Le Boulengé-Nguyen and Le Boulengé (1986). Such rates could introduce biases in the estimates of population size, survival, recruitment and trappability, which are all dependent on the assumption that all marks are retained (Seber 1982).

All lost tags were replaced in the field. For data analysis, nevertheless, two different procedures were used to deal with the problem of tag loss, according to the parameters being estimated.

1) For all estimates of home ranges, movements and spatial distributions (Chapters 4-6), tag replacements were ignored: individuals which had lost a tag were considered as new individuals. The effect of this procedure is that estimates of those parameters are likely to be conservative (e.g. some movements went undetected because of lost tags). Every location/movement quoted is based on positive evidence only.

2) For all estimates of demographic parameters (population sizes, survival, recruitment and trappability; Chapters 3-6), tag replacements were included: the code of the new (replaced) tag was applied retrospectively to an individual which had disappeared from the population previously. In other words, an individual was chosen as the "most likely" to be the one that had lost the tag. This choice was made by following, sequentially, a series of criteria, namely: 1, same species; 2, same sex; 3, same grid; 4, most recently disappeared; 5, weight equal or nearest lower; 6, similar reproductive condition. Candidates for replacement were chosen using "calendars of catches" (Petrucewicz and Andrzejwski, 1962, quoted in Le Boulengé, 1987) in which each capture was labelled with the information relevant for each criterion. Such calendars were produced using the program CMR (Le Boulengé, 1985, 1987). In the specific case of recruitment, the above procedure resulted in any individual which had lost a tag being excluded from the estimate, i.e., recruitment rates were based on new individuals only.

It is likely that in some cases of replacement the individual which actually lost the tag may have been misidentified. However this does not seriously affect estimates of population, rather than individual, parameters. For example, in a survival estimate what matters is the proportion of previously marked individuals which are still alive, not who they are. The fourth criterion (most recently disappeared) was especially relevant for survival estimates: its aim was to minimize the bias caused by "resuscitating" dead

individuals through tag replacement. As in the case of movements, I opted for a conservative option, which resulted in minimum estimates for survival.

2.3 - The data base

The analyses discussed in the following Chapters are based on the results of 22,041 trap-nights spent during the study as a whole. From this trapping effort I obtained 4,034 captures of 1,270 individual rodents. The data base for each Chapter overlaps with that of other Chapters; for example, the captures obtained in the Corner Complex (Chapters 4-6) in certain months were included in the larger scale rodent censuses carried out in those months (Chapter 3). The distribution of captures among the three rodent species is shown in Table 2.1.

TABLE 2.1. The data base: number of individuals caught and number of captures of each rodent species during the study as a whole. Data on number of individuals are corrected for tag losses (see Section 2.2.2).

Species	Individuals	Males	Females	Unsexed	Number of captures
Apodemus sylvaticus	956	549	388	19	3,172
Clethrionomys glareolus	283	133	143	7	815
Microtus agrestis	31	15	16	0	47

In addition to the rodents, there were 46 captures of common shrews (*Sorex araneus*), 13 of pigmy shrews (*S. minutus*) and four of weasels (*Mustela nivalis*).

All the figures above exclude the data from the associated studies quoted with the authors' permission, i.e., those of Gibson (1989), Harrison (1990), Vadher (1990) and Burrows (1991).

2.4 - Statistical Analysis

The statistical procedures used in this study follow Zar (1984), except when stated otherwise. Preference was given to parametric tests, but in cases where data violated the necessary assumptions I used non-parametric tests instead. Calculations were carried out using both the mainframe computer and IBM PC's at the University of Durham, plus the mainframe computer at Université Catholique de Louvain, Belgium. Commoner statistical tests were carried out using the PC program Microstat (Ecosoft, Inc.); the software used for more specific procedures is given in each of the corresponding Sections in Chapters 3 to 6. Thoughout the text results are referred to as being significant or not; this concerns statistical significance at the 5% level.

CHAPTER 3

SUCCESSIONAL AND SPATIAL VARIATION IN RODENT COMMUNITIES IN SITKA SPRUCE PLANTATIONS IN HAMSTERLEY FOREST

3.1 - Introduction

The goals of the study described in this Chapter were as follows.

(1) To characterize the overall pattern of change of species composition and relative abundances in rodent communities during succession in Sitka spruce plantations at Hamsterley Forest.

(2) To quantify the spatial (inter-site) and temporal (interannual) variation found within each successional stage.

(3) To characterize the changes in vegetation composition and structure occurring during succession.

(4) To relate the average abundance of each rodent species to the successional changes (3), to the variability in space and time found within each stage (2) and to the distribution of the other rodent species.

3.1.1 - The chronosequence approach and its assumptions

Successional changes in vegetation and their associated mammalian communities may happen over time intervals longer than most feasible studies, sometimes longer than the investigator's own life span. One way of tackling this problem is to sample simultaneously several sites at different successional stages. This general approach has been called the chronosequence method (Hill, 1986; Twigg *et al.*, 1989). Chronosequences have been used to study mammalian successions in continental Europe (e.g. Hansson, 1978; Wolk and Wolk, 1982) and studies in Australia have supported the validity of the method by showing that the patterns revealed were similar to those emerging from long-term studies following succession in a single site (Twigg *et al.*, 1989; Fox, 1990). The present Chapter reports the results of a chronosequence study of successional changes in rodent communities in Sitka spruce at Hamsterley Forest.

Implicit in the chronosequence method are two assumptions: 1) that sites are true replicates of each other (i.e., given time enough, a young plantation in my study would

develop into a habitat similar to a mature plantation as found today); 2) that sampling can be regarded as instantaneous in relation to the time scale of the successional change itself, i.e., a site selected to represent a given successional stage does not change to the following stage within the duration of the study.

The first assumption could be perfectly met only in a perfectly homogeneous habitat (and with the additional assumption that succession is completely deterministic). However, chronosequences can be used in heterogeneous habitats if several replicates of each successional stage are available. This enables the investigator to compare the effects of successional change and of local factors in determining the specific characteristics of the habitat at any given site. As discussed in Chapter 1, it is the balance between these two competing effects which determines the physiognomy of the habitat mosaic as a whole.

Replication is desirable in ecological studies, as variation is such an all-pervasive characteristic of all ecological systems (Hairston, 1989). However, when only one researcher is available to work with small mammals at between-grids (site) level rather than within-grid level, there are practical limitations to the feasible number of valid replicates. The chronosequence method implies a time constraint when applied to fluctuating populations: all replicate grids must be trapped at almost the same time if they are going to provide a true replication (Hurlbert, 1984). Usually some degree of compromise has to be achieved between the statistically desirable and the feasible; however, useful results have been produced in most small mammal studies even if they have had fewer replicates than some studies on other taxa (Schoener, 1986). The compromise must also take into account situations where greater or lesser variability is likely to be found: those demand more or less replication respectively.

3.1.2 - The chronosequence approach as applied at Hamsterley Forest

For the study reported in the present Chapter, I was able to use a "core" of eleven regularly sampled replicates representing three sucessional stages (clear-fellings, young plantations and mature plantations), plus seven additional replicates sampled occasionally (see below). Some additional, comparable data on a fourth stage, "closing" (the stage where the canopy starts to close and to shadow out the ground vegetation) were made available by an associated study in Hamsterley (Burrows, 1991). These successional stages were chosen to represent the most distinct kinds of habitats faced by rodents during succession in Sitka spruce. Numbers of replicates differed between stages, the highest number being allocated to young plantations (as high variability among them was

suggested by Gibson, 1989) and the lowest number allocated to mature plantations, which were superficially most homogeneous to a human observer.

The second assumption of the chronosequence method, that the sampling period is short in relation to the scale of successional change, may be difficult to meet when studying species with pronounced inter-annual population fluctuations, especially cyclic populations. In such cases it may be difficult to disintangle the effects of year to year differences in relative abundances from the trends associated with succession. One way of tackling this problem is to sample for several years so that year to year differences will average themselves out, but not for too many years or sites may change too much to be regarded as representative of the successional stage they were originally meant to represent. In the present study, I sampled at a standard time of the year for three years, but for the young plantations a fourth year of comparable data was available from the same sites (Gibson, 1989; see Section 3.2.1). Young plantations are the favourite habitat of *Microtus agrestis* which, in most British localities, reaches peak densities every three or four years (Elton, 1942; Chitty, 1952; Richards, 1981). Allocations of sites to given successional stages are likely to have remained valid throughout the study. Clear-felling sites were zero to three years after felling, and none of them had been replanted by the end of the study; young plantations were five to eight years after planting, and mature (first rotation) plantations were about forty years old or more. Burrows (1991) two "closing" sites were fourteen and twenty years old respectively when sampled.

As there are no second rotation mature plantations available in Hamsterley Forest I characterized succession using mature plantations of the first rotation, and clear-fellings, young plantations and "closing" stage plantations of the second rotation. This arrangement is representative of most planted forests in Britain today. My study may also be considered representative of second rotation succession, if the assumption is made that in future mature second-rotation Sitka spruce plantations will be similar to mature first-rotation ones. This assumption was discussed in Chapter 1 (Section 1.2).

3.2 - Methods

3.2.1 - Rodent censuses - Censuses were performed in early summer (early June-mid July) in 1990, 1991 and 1992. As I could not trap all grids simultaneously, census trapping was carried out during a 4-6 weeks period each year. Populations of woodmice in most forest habitats show within-year fluctuations characterized by a spring decline, numbers relatively stable in early summer (June-July), and a late summer or autumn increase (Watts

1969, Flowerdew 1985, Montgomery 1989a). Bank voles in Britain often show a similar pattern (Alibhai and Gipps, 1985); in field voles the pattern varies dramatically from year to year according to the stage of the population "cycle" (e.g. Chitty, 1952). Thus early summer data are likely to be more comparable among grids than data collected at other seasons. One of the two annual samplings for the Mammal Society survey of woodland small rodents is also performed in June (J.R. Flowerdew, pers. comm.). For these reasons, early summer was chosen as the census period. An additional "pilot" census was performed in late winter (February-March) 1990, chiefly to test whether some areas were suitable for inclusion in the regular censuses.

Standard grids were sampled regularly at ten sites during the summer censuses. three clear-fellings ("View", "Farm Felled" and "Corner South"), five young plantations ("Road", "Adder", "Stuart", "Farm Young" and "Scots Pine") and two mature plantations ("Corner North" and "Farm Mature"). Sitka spruce was the dominant conifer species in all sites, although in some mature sites a few Scots Pine (*Pinus sylvestris*) were found (mostly dead trees overshadowed by Sitka) and in some of the young plantations small amounts of Scots Pine had been planted alongside Sitka. The sites within the Corner Complex (see Chapters 4 and 5) which were clear-felled during the study ("Corner 1", "2" and "3") were included in each census according to the successional stage they presented at the time. Clear-fellings where brashings were experimentally removed (see Chapter 5) were not included in the censuses after the manipulation, because they were not considered as representative of "natural" clear-fellings anymore. Some additional grids ("Hut Mature", "Corner East", "Corner Young") were trapped only in the summer 1990 census, in association with Vadher's (1990) study. One mature site ("Adder Mature") included in the pilot census was not trapped thereafter due to frequent human disturbance to the plot. The position of all sites within Hamsterley Forest is shown in Figure 3.1.

The National Grid Reference of each site, dates of planting and/or felling, and soil types according to the Forest Comission's soil map of Hamsterley are shown in Table 3.1. It should be noticed that there is a great variation of soil types within each successional stage, and that distribution of soil types is "fine-grained" spatially, so that most sites have at least two distinct types/subtypes of soil.

S. Gibson kindly allowed me to use her original data on rodent abundances in the young plantations in 1989. Gibson's second trapping session (which I use) was performed at the same time of the year as my summer censuses, but she used five-day trapping sessions while I used three days. To correct for this, I have reworked her data to include only the first three days in each of her sessions. Even so, the data are not wholly comparable because: 1) Gibson's grids had 50 traps, while mine had 49; 2) she used two

Figure 3.1. Map of Hamsterley Forest showing the location of all study sites. Sites corresponding to each successional stage are represented by different symbols: clear-fellings (□), young plantations (Δ) and mature plantations (×). Sites Corner 1 to Corner 3, which are very close to each other, are represented together; for a more detailed map of the position of these sites, see Chapter 4.

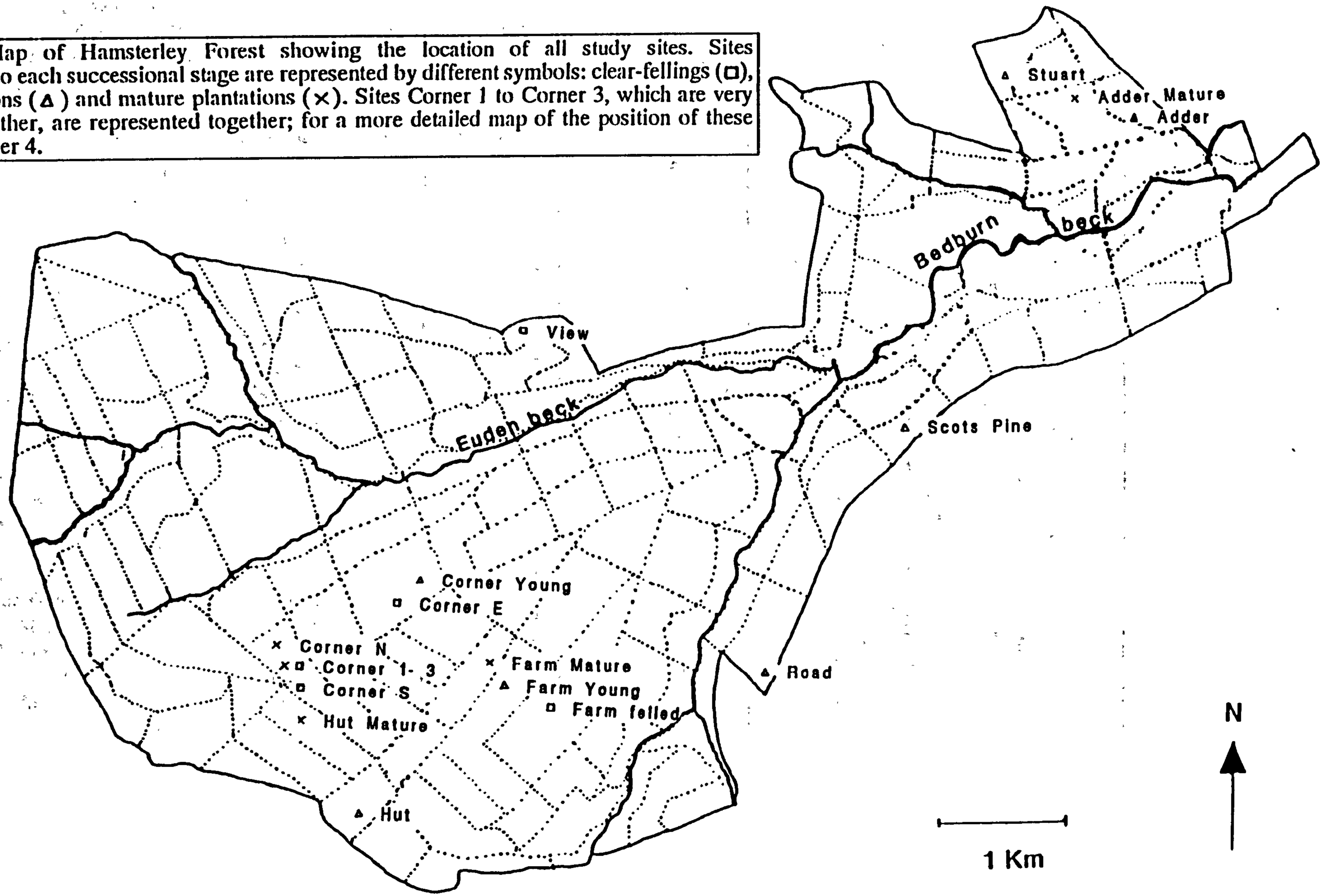


TABLE 3.1. Characteristics of the 18 sites trapped during the study: successional stage(s) surrounding each grid (CF = clear-felling), National Grid Reference, dates of planting (Pl.) and of clear-felling (Fel.), and soil types according to the classification used in Forestry Commission's soil map of Hamsterley. In the soil types, species forming the bogs are: Cv, *Calluna vulgaris*; Ev, *Eriophorum vaginatum*; Je, *Juncus effusus*. Two different grids were used on Hut site during the study (see text).

Site	Successional stage(s)	National grid reference	Dates of planting / felling	Soil type(s)
Farm Felled	CF	NZ 048 279	Fel 1989	podzolic gley / peaty gley
View	CF	NZ 045 302	Fel 1989	podz. gley
Corner South	CF	NZ 033 280	Fel 1989	ironpan / Cv, Ev blanket bog
Corner East	CF	NZ 038 286	Fel 1990	podz. gley / peaty gley
Corner 1	Mature / CF	NZ 032 281	Pl 1946, Fel 1990	surface-water gley / podz. gley
Corner 2	Mature / CF	NZ 032 283	Pl 1946, Fel 1990	peaty gley / Cv, Ev blanket bog
Corner 3	Mature / CF	NZ 033 282	Pl 1946, Fel 1990	surface-water gley / podz. gley
Hut	Young	NZ 037 272	Pl 1984	surface-water gley / podzolic gley
		NZ 035 272	Pl 1986	brown earth / brown gley / podz. gley
Adder	Young	NZ 084 315	Pl 1984	surface-water gley
Farm Young	Young	NZ 046 281	Pl 1984	podz. gley / typical podzol /Je bog
Scots Pine	Young	NZ 073 296	Pl 1984	ironpan / brown earth
Road	Young	NZ 061 280	Pl 1985	brown gley / ironpan / brown earth
Stuart	Young	NZ 077 317	Pl 1985	surface-water gley
Corner Young	Young	NZ 041 287	Pl 1986	podz. gley / typical podzol
Adder Mature	Mature	NZ 082 315	Pl 1927	surface-water gley
Hut Mature	Mature	NZ 032 278	Pl 1945-48	peaty gley / Cv, Ev blanket bog
Corner North	Mature	NZ 031 284	Pl 1946	Cv, Ev blanket bog
Farm Mature	Mature	NZ 045 282	Pl 1954	podz. gley / typical podzol

days of pre-baiting, while I did not use pre-baiting; 3) she used rectangular (5 x 10 points) grids, while I used square (7 x 7) grids. While the first difference is likely to be negligible, the other two might be important. Both of these methodological differences are likely to produce a greater edge effect in her grids and thus inflated population estimates when compared with mine. Edge effect is a recurrent problem for estimation of small mammal densities in general (Smith *et al.*, 1975; Flowerdew, 1976). For this reason Gibson's results were used only when comparing relative abundances of the three rodent species.

In order to simplify the interpretation of some comparisons, two data sets were defined. The "**restricted data set**" (shown in **bold** in all Tables) excludes the results of the pilot (late winter) census and all the "one-offs" (grids trapped just once in the summer censuses). The results of the pilot census as well as the one-offs form the "additional data set". The two sets put together are referred to as "total data".

3.2.2 - Analysis of rodent distributional patterns - The abundances of the rodent species at the time of each census in each site were estimated by the number of different individuals captured. The one-year time intervals between most censuses and the short duration of each trapping session prevented the use of probabilistic population estimators, which are dependent on survival and/or catchability estimates. Most individuals marked in one year would have died by the next.

For each rodent species separately, abundances in the three years (four for young plantations) were compared by means of analysis of variance (one-way ANOVA, Zar, 1984). In ANOVA's terminology, the groups were defined by all sites trapped in each year, irrespective of successional stage. The restricted data set was used in this analysis. The frequency distributions of abundances amongst the sites of two of the rodent species (*Microtus agrestis* and *Clethrionomys glareolus*) showed significant positive skewness and therefore they were normalised by $x' = \log (x + 1)$ transformations prior to the analysis.

For each rodent species, abundances in different sites within each successional stage were compared as well. In ANOVA's terminology, each group was defined by one site, the members of each group being the numbers captured in that site in each of the years. As above, the restricted data set was used. Given the low number of elements (years) in each group and the consequent impossibility of reliably assessing the normality of the data, the non-parametric Kruskal-Wallis test (Zar, 1984) was used. For comparing abundances in different mature plantations, of which only two replicates were available in the restricted data set, a non-parametric Mann-Whitney U test (Zar, 1984) was used instead of Kruskal-Wallis.

Pairwise correlations between the abundances of the rodent species were tested using Pearson's product-moment correlations (Zar, 1984). For this analysis the total data set was used, as the aim was to test how the abundances of each pair of species were correlated over a range of different circumstances.

3.2.3 - Diversity and Evenness - Diversity was estimated using the modified Shannon index, $e^{H'}$, where e = basis of the natural logarithms, $H' = \sum pi.\ln(pi)$ and pi = proportion of the species "i" in the sample. Compared to the original Shannon index (H'), which is proportional to the logarithm of the number of species, $e^{H'}$ has the advantage of being directly proportional to the number of species itself, which makes interpretation easier. For example, a community with $e^{H'} = 3$ has a diversity equivalent to three equally abundant species (Ludwig and Reynolds, 1988).

Evenness, one of the components of diversity, was estimated separately using Hill's modified ratio (Alatalo, 1981). The aim of this procedure was to separate the effects of species richness and of variations in the distribution of relative abundances when interpreting the diversity patterns. In relation to other evenness indices, Hill's modified ratio has the considerable advantage that it tends to be independent of sample size (Ludwig and Reynolds, 1988) and it is given by (terminology as above):

$$E = \frac{(1/\sum p_i^2) - 1}{e^{H'} - 1}$$

Computations of diversity and evenness indices were performed using Ludwig and Reynolds' (1988) "Statistical Ecology" program.

When Shannon's and Hill's indices are calculated for a set of sites many of which contain just one species, they tend to generate a strongly bimodal distribution, where one mode is the value corresponding to an one-species community (Shannon's index = 1 and Hill's = 0). Such distributions cannot be made normal by the usual data transformations, and therefore when comparing the indices I used non-parametric Mann-Whitney U tests instead of t-tests. The data from the winter census were discarded in these tests, to minimize the effects of population fluctuations on the comparisons of diversity and evenness.

3.2.4 - Habitat Description - All habitat analysis were performed at among-grids level rather than within-grid level, i.e., although each grid is represented by the sum of several

sampling / trapping points, the grid as a whole was the basic unit of analysis throughout. The habitat variables measured included those which were shown to be important for at least one of the axes identified through Principal Component Analysis of habitats in young second-rotation plantations by Gibson (1989). Several other variables which I suspected to be important for other stages were added as well, making a total of 20 habitat variables divided into two sets: 10 variables describing cover by different plants in the associated vegetation, and 10 structural variables. The variables measured are listed in Table 3.2. The variable "palatable grasses" includes all the species of soft grasses found in the study sites and known to be good food resources for *Microtus agrestis* (Ferns, 1976), but most of the records refer to three species only: *Holcus lanatus*, *Agrostis canina* and *H. mollis*.

Habitat variables were measured in fifteen sites, including all sites in the restricted data set and four additional ones, among them the two canopy closing sites (Burrows, 1991). Measurements were taken in May-June 1991. At this time of the year many plants are in flower, making identifications easier. In each plot, most variables were measured in nine 1 m^2 quadrats distributed along the grid, one in the center, four making a cross around this first one, and one near each corner of the grid (Figure 3.2). This technique was adapted from Shimwell (1971) and aims to provide homogeneous cover of areas where gradients may be present. For the plant cover variables, numerical values were attributed to each using the Domin scale, which varies from 0 to 10 with increasing percentage cover (Bannister, 1966; Chapman, 1976). The structural variables describing cover were measured directly in percentages rather than on the Domin scale, and the measurement of a few other structural variables followed specific procedures. Height of undergrowth was sampled in the 1m^2 quadrats, but measured in cm. For the four density variables (cones, Sitka trees, broadleaved trees, Sitka saplings) and for cover by low branches it was felt that a larger sampling area was required to produce meaningful estimates. These variables were measured in a circle with a ratio of 2.5 m (area 19.65 m^2) centered at the cane marking the point. Cones, trees and saplings were counted and percent cover by low branches estimated within such circles. The use of different scales to measure different variables does not matter for the ordination techniques, DCA and CCA (see below), because the variables are standardized during the calculations (see case studies in Ter Braak, 1986).

Analysis of the successional changes and their relationships with the rodent abundances followed two steps, using two complementary multivariate methods. First the changes in vegetation were studied by means of ordinations using Detrended Correspondence Analysis or DCA (Hill and Gauch, 1980; Gauch, 1982). DCA ordinates sites or species along environmental gradients, by creating axes which are composites of

TABLE 3.2. Habitat variables measured in fifteen of the Census grids. Asterisks (*) indicate those measured also by Gibson (1989). Variables were measured using the Domin scale (see text) except where specified otherwise.

PLANT COMPOSITION VARIABLES

1) Purple moor grass (*Molinia caerula)**

2) Palatable grasses (*Agrostis canina, A. capillaris, Holcus lanatus, H. mollis, Festuca ovina*) *

3) Wavy hair grass (*Deschampsia flexuosa*)*

4) Heather (*Calluna vulgaris*) *

5) Bracken (*Pteridium aquilinum*) *

6) Bramble (*Rubus fruticosus*) *

7) Bilberry (*Vaccinium myrtillus*)*

8) Herbs (e.g. *Chamaenerium angustifolium, Galium saxatile, Rumex* spp) *

9) Rushes (*Juncus effusus, J. squarosus*) *

10) Mosses

STRUCTURAL VARIABLES

11) Height of ground vegetation (cm)

12) Total cover by ground vegetation (%)

13) Cover by bare soil (%)*

14) Cover by litter (%)

15) Density of spruce cones on the ground (number/m^2)

16) Cover by brashings * (%)

17) Density of Sitka spruce trees* (number in a 5m diameter circle)

18) Density of broadleaved trees * (as above)

19) Cover by low branches (%)

20) Density of Sitka spruce saplings (number/m^2)

Figure 3.2. Diagram of a standard trapping grid, with 15m trap spacing (see text, Chapter 2). Trapping was performed at all points, and habitat sampling was performed at the nine points marked by squares.

environmental variables (indirect gradient analysis). Calculations were performed using the program DECORANA (Hill, 1979a), separately for the two sets of measured habitat variables, i.e., the plant cover variables and the structural variables. For each set of variables, ordinations of the sites according to the habitat variables and of the variables according to the sites were calculated ("samples" ordination and "species" ordination respectively in DCA terminology). The sites were plotted in relation to the first two axes in a two-dimensional plot, using the "sample scores" produced by the program. Sites close together in the plot are similar in terms of the cover/structural variables measured; those far apart are dissimilar. Successional stage and habitat data collected from the sites were then used to interpret the gradients. Reciprocally, habitat variables were ordinated by site using DCA's "species scores". Variables close together in the plot have a similar distribution across sites.

The second step was to relate the whole pattern of variation of vegetation (cover and structural) with the abundances of the rodents, sitewise, to identify the environmental factors which are correlated with the observed abundance of rodents at different stages. This analysis used Canonical Correspondence Analysis or CCA (Gauch, 1982; Ter Braak, 1986). CCA has the advantage that the ordination axes are chosen in the light of known environmental variables, by imposing the extra constraint that axes are linear combinations of known environmental variables (direct gradient analysis). In CCA terminology, the habitat variables were treated as "environmental constraints" and the rodent abundances were treated as "biological response". Calculations were performed by the program CANOCO (CANOnical Community Ordination; Ter Braak, 1988). All variables (plant cover and structural) were pooled together in the initial set of variables (allowing insights into the relative importance of plant cover and structural variables). Before running CCA itself, the Variable Inflation Factors (VIF) and weighted correlation coefficients were analysed in order to detect and remove variables which were too closely correlated to be used together in the ordination (see Ter Braak, 1986).

3.3 - Results

3.3.1 - Overall patterns in species composition, numbers and relative abundances - The numbers of different individuals caught for each species at each site during each census are shown in Table 3.3. These data include S. Gibson's 1989 data.

The proportions of the three species in the restricted data set and the additional data set did not differ significantly for young plantations and mature plantations (Table

TABLE 3.3. Abundances of three species of rodents at 19 sites, and totals recorded in each successional stage. In each series of three numbers, the first refers to *Apodemus sylvaticus*, the second to *Clethrionomys glareolus* and the third to *Microtus agrestis*. The restricted data set (see text) is shown in **bold.**

Successional stages	Site	Summer 1989 *	Winter 1990	Summer 1990	Summer 1991	Summer 1992	Totals: **Restricted data set** + additional data set Total data	Comparing proportions of the rodent species: **restricted data set** and additional data set
Clear-fellings	Farm Felled		**16-1-0**	**10-0-0**	**9-0-0**	**0-0-1**		
	View		**19-4-0**	**9-2-0**	**12-3-0**	**4-1-0**	**75-30-1**	
	Corner South			**9-0-0**	**6-0-0**	**0-1-0**	**+ 49-6-0**	$X^2 = 5.48$, 1 d.f., $p < 0.05$
	Corner 2				**14-3-0**	**2-20-0**	124-36-1	
	Corner East			**7-0-0**				
	Corner 3				**7-1-0**			
Young (5-8 yrs old)	Hut	**3-5-3**	**6-2-3**	**20-7-0**				
	Adder	**6-3-0**	**11-1-1**	**8-0-0**	**7-0-0**	**8-0-0**		
	Farm	**5-66-4**	**6-19-0**	**13-22-0**	**18-7-0**	**1-8-0**	**104-118-76**	
	Scots Pine	**1-0-10**	**0-1-2**	**4-0-0**	**2-0-0**	**1-3-1**	**+ 54-52-9**	$X^2 = 0.33$, 2 d.f., $p > 0.75$
	Road	**0-0-50**		**7-0-1**	**4-1-3**	**0-7-7**	158-170-85	
	Stuart	**10-0-0**		**4-0-0**	**7-1-0**	**7-0-0**		
	Corner Young			**8-17-0**				
Mature (about 40 yrs old or more)	Adder Mature		**15-0-0**					
	Corner 1		**1-0-0**	**3-1-0**				
	Corner 2		**10-2-0**	**9-5-0**			**70-31-0**	
	Hut Mature			**13-5-0**			**+51-13-0**	X2 = 1.66, 1 d.f., $p > 0.10$
	Corner North			**5-6-0**	**31-9-0**	**4-8-0**	121-44-0	
	Farm Mature			**2-6-0**	**27-2-0**	**1-0-0**		

* Data from Gibson (1989).

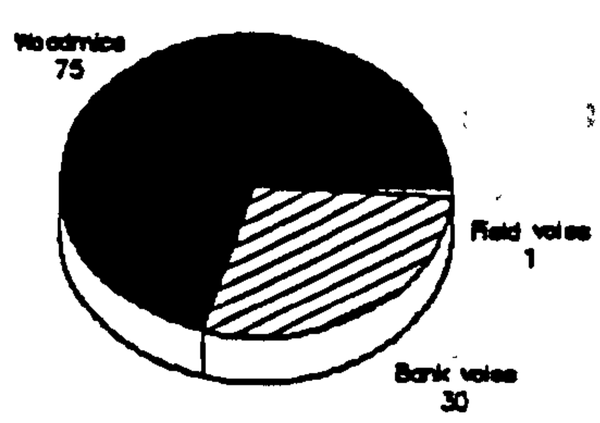
3.4). Therefore, the total data set was used to represent the proportions of the three species in both these successional stages. On the other hand, the proportions in the two data sets differed significantly ($X^2 = 5.48$, $p < 0.05$; Table 3.3) in the clear-fellings. Therefore, the restricted data set was used to represent the proportions at this stage.

Figure 3.3 shows how the individuals captured are distributed among the three rodent species in each of the successional stages, pooling data from all sites representing each stage. In addition to the stages described above, Figure 3.3 includes the "closing" stage data from Burrows, 1991, who used exactly the same study methods as I did. Two patterns are imediately apparent: (1) field voles were present in considerable abundance in young plantations, but virtually absent in the other stages; and (2) the proportions of woodmice to bank voles were quite variable among different stages. At clear-fellings, woodmice were by far the dominant species and bank voles were much less abundant (throughout this study, "dominant" is used simply as a short-cut to "the most abundant species"). In young plantations as a whole abundances of these two species were quite equitative, the proportion of bank voles to woodmice being significantly higher in this stage than in both clear-fellings and mature plantations (see Table 3.4, below). The pattern for the "closing" stage (represented by much smaller sample sizes) resembles the young plantations, with high abundance of bank voles; the proportions of the two species did not differ significantly from young plantations (Table 3.4). Mature plantations overall presented a pattern which resembles clear-fellings', from which they did not differ significantly (Table 3.4).

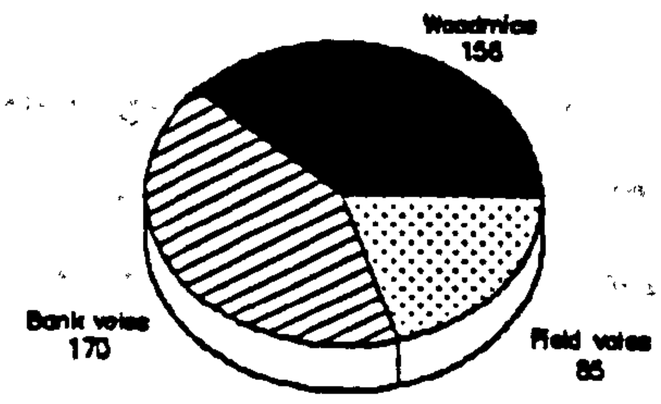
TABLE 3.4. Comparisons of the ratio of woodmice to bank voles in different successional stages. Data from Figure 3.3. Chi-square tests with one degree of freedom and Yates correction for continuity.

Successional stages: comparison	X^2	Significance* (2-tail)
Clear-fellings x Young	16.39	$p < 0.001$
Clear-fellings x Closing	0.69	$p > 0.25$
Clear-fellings x Mature	0.04	$p > 0.75$
Young x Closing	2.99	$0.05 < p < 0.10$
Young x Mature	13.20	$p < 0.001$
Closing x Mature	1.38	$p > 0.10$

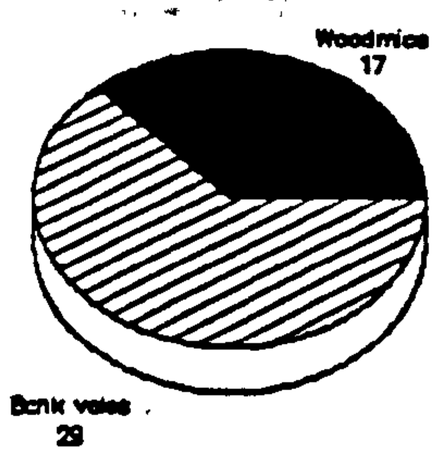
FIGURE 3.3. Pie charts of the distributions of abundances (number of different individuals captured) of the three rodent species in plantations of four successional stages, pooling all the sites of each stage. Data from Table 3.3, except on the "closing" stage which are from Burrows (1991). The **restricted data set** was used for clear-fellings, and the total data set for the remaining stages (see text).



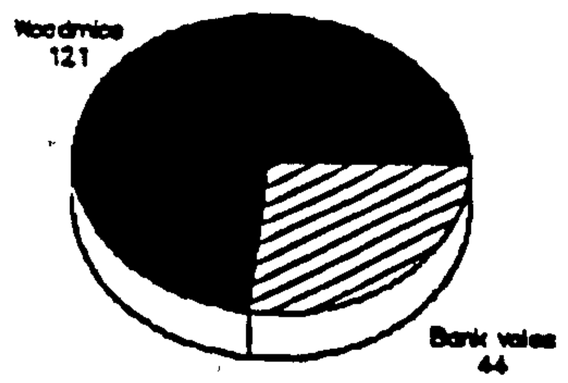
Clear–Fellings



Young Plantations



"Closing" stage



Mature Plantations

Total numbers of rodents at each site (the sum of the three numbers of the sequences in Table 3.3) were compared across stages. Analysis was based on the total data set, but excluding Gibson's 1989 data because of the bias expected from the methodological differences pointed out above, and the winter 1990 pilot census because of the effects of seasonal variation in numbers. Although the average total number of rodents was highest in mature plantations followed by young plantations and clear-fellings, values were quite variable within each successional stage and consequently t-tests did not show any significant difference between any of the stages (Table 3.5).

TABLE 3.5. Averages of the total number of rodents caught in a summer standard trapping session at each successional stage (top) and comparisons among the stages (bottom). Data from Table 3.3 with some deletions (see text). Logarithmic transformations were used to normalise the data prior to the tests.

Successional stage	Number of trapping sessions	n ± s.d.
Clear-fellings	13	9.31 ± 5.99
Young	17	12.00 ± 9.72
Mature	09	15.22 ± 12.36

Comparisons	t	Significance (p) (2-tail)
Clear-fellings x Young	-0.7869	0.2190
Clear-fellings x Mature	-0.9925	0.1664
Young x Mature	-0.4563	0.3262

3.3.2 - Temporal variation and spatial variation - The average abundances of woodmice and of field voles were found to be significantly different in the four years from 1989 to 1992 (ANOVA, woodmice $F = 5.640$, $p < 0.01$, and field voles $F = 5.640$, $p < 0.01$). However, no significant difference was found amongst years in the average abundance of bank voles (Table 3.6, top).

TABLE 3.6. Top: ANOVAs comparing for each species of rodent the numbers captured in different years at all sites trapped. Bottom: Kruskal-Wallis test for each successional stage comparing the numbers of each species captured per site. Each site was represented by numbers caught in all years when that site was trapped. Both analyses used the restricted data set (see text). For mature plantations (1 d.f.), Mann-Whitney's U-test was used; values of z (the normal aproximation to Mann-Whitney's U statistics) are shown.

Species	Source of variation	Mean square	D.F.	Mean square	F	Significance of F
Apodemus sylvaticus	Among years	579.42	3	19.139	5.64	$p < 0.01$
	Within years	1129.56	33	34.229		
	Total	1708.97	36			
Clethrionomys glareolus	Among years	0.13	3	0.043	0.17	$p = 0.92$
	Within years	8.47	33	0.257		
	Total	8.61	36			
Microstus agrestis	Among years	1.70	3	0.566	5.64	$p < 0.01$
	Within years	3.31	33	0.101		
	Total	5.01	36			

Species	Successional stages	H	D.F.	Significance (p)
Apodemus sylvaticus	Clear-fellings	1.076	3	0.7829
	Young	8.489	4	0.0752
	Mature	(z) 1.091	1	0.1376
Clethrionomys glareolus	Felled	7.746	3	0.0516
	Young	9.329	4	0.0534
	Mature	(z) 1.746	1	0.0404
Microtus agrestis	Young	8.146	4	0.0864

Differences in rodent abundance among sites (within a given successional stage) were found to be significant only for bank voles in mature plantations (Mann-Whitney test, 2-tail, $z = 1.746$, $p < 0.05$; Table 3.6, bottom). However, the overall pattern shown in Table 3.6 (bottom) should be interpreted carefully: while only this difference was significant, $0.05 < p < 0.10$ was found in not less than four out of the six remaining comparisons.

3.3.3 - Correlations among the abundances of the rodent species - No significant correlation was found between the abundance of bank voles and either of the other two species (Table 3.7). On the other hand, a significant negative correlation between the abundance of woodmice and of field voles was found in young plantations ($r = -0.344$, $n = 27$, $p < 0.05$).

TABLE 3.7. Values of Pearson's coefficients (r) for the correlations between the abundances of rodent species in different sites in each successional stage. Number of sites for each stage is indicated (n's) and significance of the values is shown following each r; n.s. = non significant; * = $p < 0.05$.

Species: comparison	Clear-fellings (n = 15)	Young (n = 27)	Mature (n = 12)
A. sylvaticus x *C. glareolus*	-0.150 (n.s.)	0.090 (n.s.)	0.271 (n.s.)
A. sylvaticus x *M. agrestis*	-0.413 (n.s.)	- 0.344 *	-
C. glareolus x *M. agrestis*	-0.132 (n.s.)	-0.057 (n.s.)	-

3.3.4 - Diversity and evenness - When data from all sites at each successional stage were pooled (as in Figure 3.3), young plantations have a higher rodent diversity, as measured by Shannon index, than either clear-fellings or mature plantations. Those two latter stages presented similar diversities (Table 3.8, last column). However, when instead of pooling the data diversity indices were calculated on a site-by-site basis (Table 3.8), a very different picture arose. On a site-by-site basis Shannon indices were not significantly higher in young plantations than in either of the remaining two stages, while site diversities in mature plantations were significantly higher than in clear-fellings (Table 3.10).

TABLE 3.8. Shannon's $e^{H'}$ diversity indices for the rodent community at each site, based on data from Table 3.3. For the pooled values (last column) data for all sites of a given stage were put together and the diversity indexes calculated from the resulting set of pooled abundances. Remaining symbols as in Table 3.3.

Successional stages	Site	Summer 1989	Winter 1990	Summer 1990	Summer 1991	Summer 1992	Pooled (all sites of each stage put together)
Clear-fellings	Farm Felled		1.2507	1	1	1	1.7640
	View		1.5873	1.6066	1.6494	1.667	
	Corner South			1	1	1	
	Corner 2				1.5936	1.3561	
	Corner East			1			
	Corner 3				1.4576		
Young	Hut	2.9069	2.7045	1.7723			2.8815
	Adder	1.8899	1.7091	1	1	1	
	Farm Young	1.5673	1.7351	1.9342	1.8093	1.4174	
	Scots Pine	1.3561	1.8899	1	1	2.5864	
	Road	1		1.4576	2.6494	2.0000	
	Stuart	1		1	1.4576	1	
	Corner Young			1.8717			
Mature	Adder Mature		1				1.7859
	Corner 1		1	1.7548			
	Corner 2		1.5692	1.9189			
	Hut Mature			1.8055			
	Corner N			1.9917	1.7043	1.8899	
	Farm Mature			1.7548	1.1534	1	

TABLE 3.9. Hill's modified evenness indices for the rodent community at each site, based on data from Table 3.3. For the pooled values (last column) data for all sites of a given stage are put together and the evenness indexes are calculated for the resulting set of pooled abundances. Remaining symbols as in Table 3.3.

Successional stages	Site	Summer 1989	Winter 1990	Summer 1990	Summer 1991	Summer 1992	Pooled (all sites of each stage put together)
Clear-fellings	Farm felled		0.5318	0	0	0	0.7330
	View		0.7311	0.8019	0.8034	1.0266	
	Corner S			0	0	0	
	Corner 2				0.7527	0.5881	
	Corner E			0			
	Corner 3				0.7285		
Young	Hut	1.2782	1.1116	0.8591			0.9590
	Adder	1.1237	0.5897	0	0	0	
	Farm	0.5008	0.8337	0.9907	0.8947	0.6845	
	Scots Pine	0.6240	2.2475	0	0	1.4708	
	Road	0		0.7285	1.2800	1.1667	
	Stuart	0		0	0.7285	0	
	Corner young			0.9513			
Mature	Adder mature		0				0.8256
	Corner 1		0	1.3249			
	Corner 2		0.7639	1.0646			
	Hut mature			0.9170			
	Corner N			1.2100	0.7907	1.0576	
	Farm mature			0.9937	0.5378	0	

The same contrast of the patterns for pooled and site-by-site indices was found again when the evenness component of diversity was analysed separately. When sites were pooled, Hill's evenness index was still highest for young plantations, followed by mature plantations and clear-fellings in this order (Table 3.9). However, when indices were calculated on a site-by-site basis (Table 3.9), again Hill's indices were not significantly higher in young plantations than in either of the two other stages, while mature plantations had a significantly higher site evenness than clear-fellings (Table 3.10).

TABLE 3.10. Comparison of the site diversity and site evenness indices of different successional stages, by means of Mann-Whitney's U tests. Data from Tables 3.8 and 3.9, using data from the summer censuses only. The statistics quoted are 1-tail values of z, the normal aproximation to the Mann-Whitney distribution, and their significance (see text).

Comparison	Diversity indices: z and significance	Evenness indices: z and significance
Clear-fellings x young	-1.334 ($p = 0.091$)	-1.1563 ($p = 0.125$)
Clear-fellings x mature	-2.871 ($p < 0.01$)	-2.538 ($p < 0.01$)
Young x mature	-0.901 ($p = 0.184$)	-1.551 ($p = 0.061$)

3.3.5 - Patterns of successional change and their relationship with the rodents - The values measured for each habitat variable at each site are presented in Table 3.11. Each value in Table 3.11 is the average of the nine measurements taken at each site, rounded to the nearest integer. From the examination of the table itself some differences among successional stages can easily be noted. For example, the plant cover variables (1-9, 12) had consistently low values in clear-fellings and in mature plantations, while cover by brashings (variable 16) was high in recent clear-fellings, intermediate in young plantations and low in the older sites.

In the analysis by DCA, the eigenvalues for the four ordination axes for plant cover were 0.177, 0.135, 0.041 and 0.011, and for structure were 0.520, 0.285, 0.076 and 0.019. These results show that in both cases the first two axes accounted for most of the

TABLE 3.11. Average values for the twenty habitat variables at each of the fifteen rodent trapping sites in Hamsterley Forest. Measurements were taken at nine points in each site (see Section 3.2.4). For description of the variables and units, see Table 3.2. Data for the "Closing" stage are from Burrows (1991). The second column refer to the variables deleted prior to CCA because of intercorrelations (see text, Section 3.2.4). Codes for the sites are: C1-C3, Corner 1-3; FF, Farm Felled; CS, Corner South; Vi, View; Sc, Scots Pine; Ro, Road; Ad, Adder; St, Stuart; Fy, Farm Young; LC, Burrows' Low Closing; HC, Burrows' High Closing; CN, Corner North; Fm, Farm Mature.

Habitat variables	Variables deleted prior to CCA	Clear-fellings						Young plantations					"Closing"		Mature	
		C1	C2	C3	FF	CS	Vi	Sc	Ro	Ad	St	Fy	LC	HC	CN	Fm
1) *Molinia caerula*		0	0	0	0	0	0	0	2	0	0	0	3	4	0	0
2) Palat. grasses		2	1	2	1	1	4	5	5	6	4	3	1	3	0	0
3) *Deschampsia flexuosa*		0	0	1	1	1	3	8	6	3	6	3	3	0	0	0
4) Heather		0	0	1	0	1	5	4	4	7	5	8	3	5	0	0
5) Bracken		0	0	0	0	0	0	4	1	0	1	0	0	4	0	0
6) Bramble		0	0	0	0	0	0	3	5	2	0	3	0	2	0	0
7) Bilberry		0	0	0	0	0	0	1	3	1	1	1	4	0	0	0
8) Herbs	*	1	0	0	2	2	4	1	4	4	3	2	2	3	0	1
9) Rushes	*	0	0	0	0	0	3	4	3	3	2	3	0	2	0	0
10) Moss		3	2	2	3	2	3	5	5	5	4	5	5	5	3	6
11) Height undergrowth	*	3	0	4	5	13	11	19	21	23	19	31	12	16	0	1
12) Cover undergrowth	*	1	0	1	1	1	26	70	59	70	52	57	19	24	0	1
13) Bare soil		18	8	0	3	11	5	0	0	0	3	3	0	0	0	3
14) Cover by litter	*	54	34	50	27	63	3	3	11	0	0	3	55	39	70	54
15) Density of cones	*	1	15	2	3	1	1	0	0	0	0	0	0	0	43	3
16) Cover by brashings		4	57	52	65	19	40	3	16	6	21	16	1	5	7	14
17) Density of Sitka		0	0	0	0	0	0	4	5	4	7	31	3	3	5	2
18) Density broadleaved		0	0	0	0	0	0	1	1	10	3	1	1	2	0	0
19) Dens. low branches		0	0	0	0	0	5	9	2	9	9	44	57	40	59	41
20) Dens. Sitka saplings	*	1	0	0	1	1	21	3	2	9	5	23	0	0	0	0

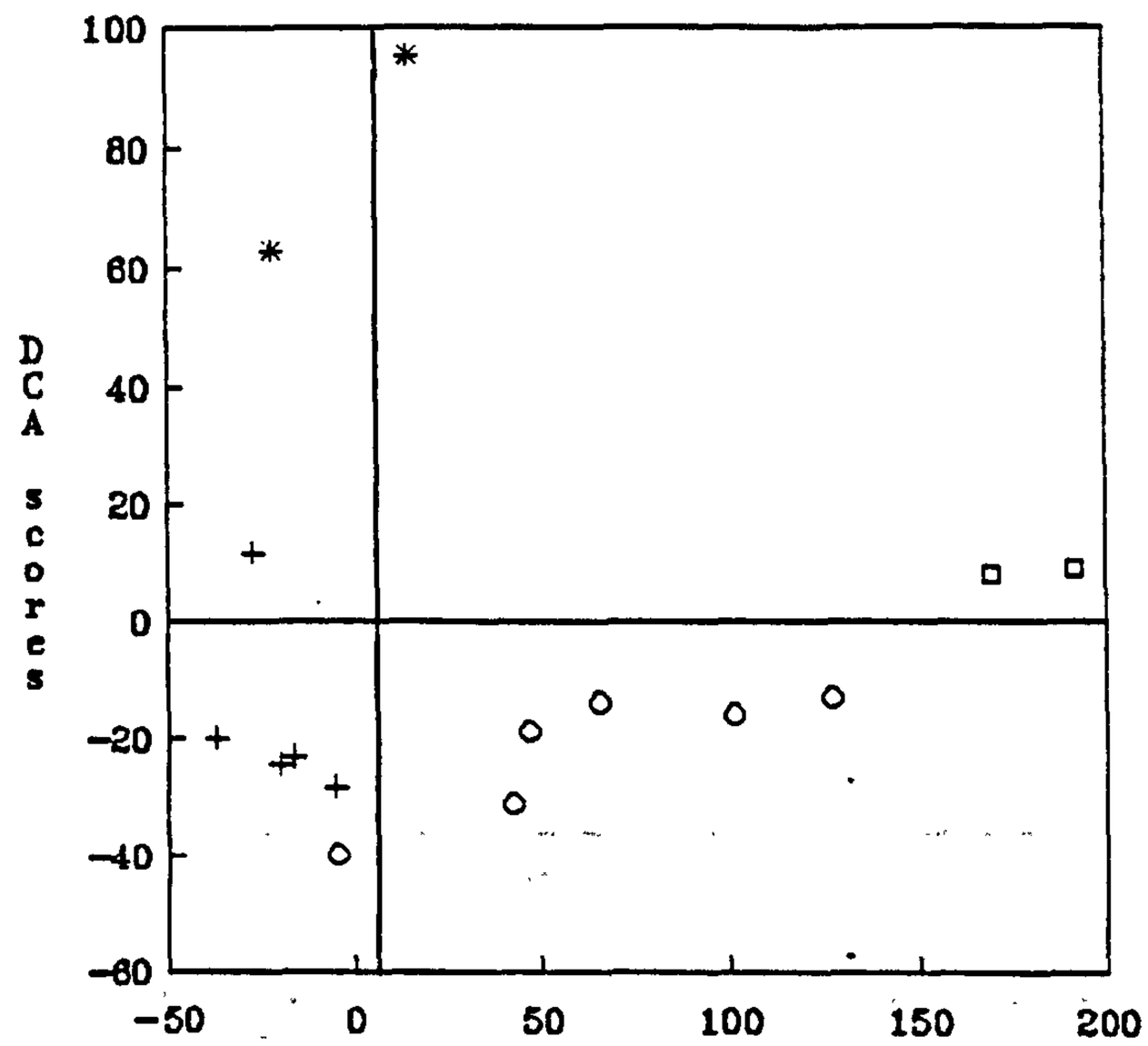
variation explained by the ordination, while the remaining axes explained little of the variation and will not be discussed further. The eigenvalues also show that DCA accounted for a greater proportion of the variation in structure than in plant cover.

The four DCA plots (ordination of sites and ordination of habitat variables, for each set of variables) are presented in Figures 3.4 to 3.7. The respective DCA scores are presented under each plot to allow identification of individual sites / habitat variables in the plots. Ordination of the sites clearly separates the stages of succession, either using the plant cover variables or the structural variables. In the plot of site ordination by plant cover (Figure 3.4), succession can be visualized as a circle going clockwise around the diagram passing by the clusters which correspond to the successive stages. Only one clear-felling lay to the left of the vertical axis, and was thus more similar to young plantations than to the rest of the clear-fellings. This point corresponds to the View site, the clear-felling where colonization by ground vegetation was quickest (see variables 1-10 in Table 3.11). This explains its similarity to young plantations. In the plot of plant cover variables ordinated by sites (Figure 3.5), the position of the variables in relation to the positions of the successional stages in the previous plot provides a picture of the vegetation changes. Therefore, herbs are most associated to clear-fellings; palatable grasses appear in clear-fellings but closer to the young plantation stage of which *Deschampsia flexuosa*, heather, bracken, bramble and rush were most characteristic; bilberry was most associated to the transition between young and "closing" stages, *Molinia caerula* to the "closing" sites, and mosses were most associated to mature plantations.

In the plot of site ordination by structural variables (Figure 3.6), the pattern found in Figure 3.4 repeats itself: successional change again appears as a clockwise trajectory around the diagram, and again View is closer in character to young plantations than to clear-fellings. In the plot of structural variables ordinated by site (Figure 3.7), clear-fellings are most closely associated with bare soil and abundance of brashings but young plantations to increased cover and height of ground vegetation, and to increased density of trees (both conifer and broadleaved) and of Sitka saplings. The "closing" stage was most closely associated, as one would expect, to maximum density of low branches. Mature plantations were associated with high cover by litter (represented mostly by undecomposed Sitka needles) and density of Sitka cones.

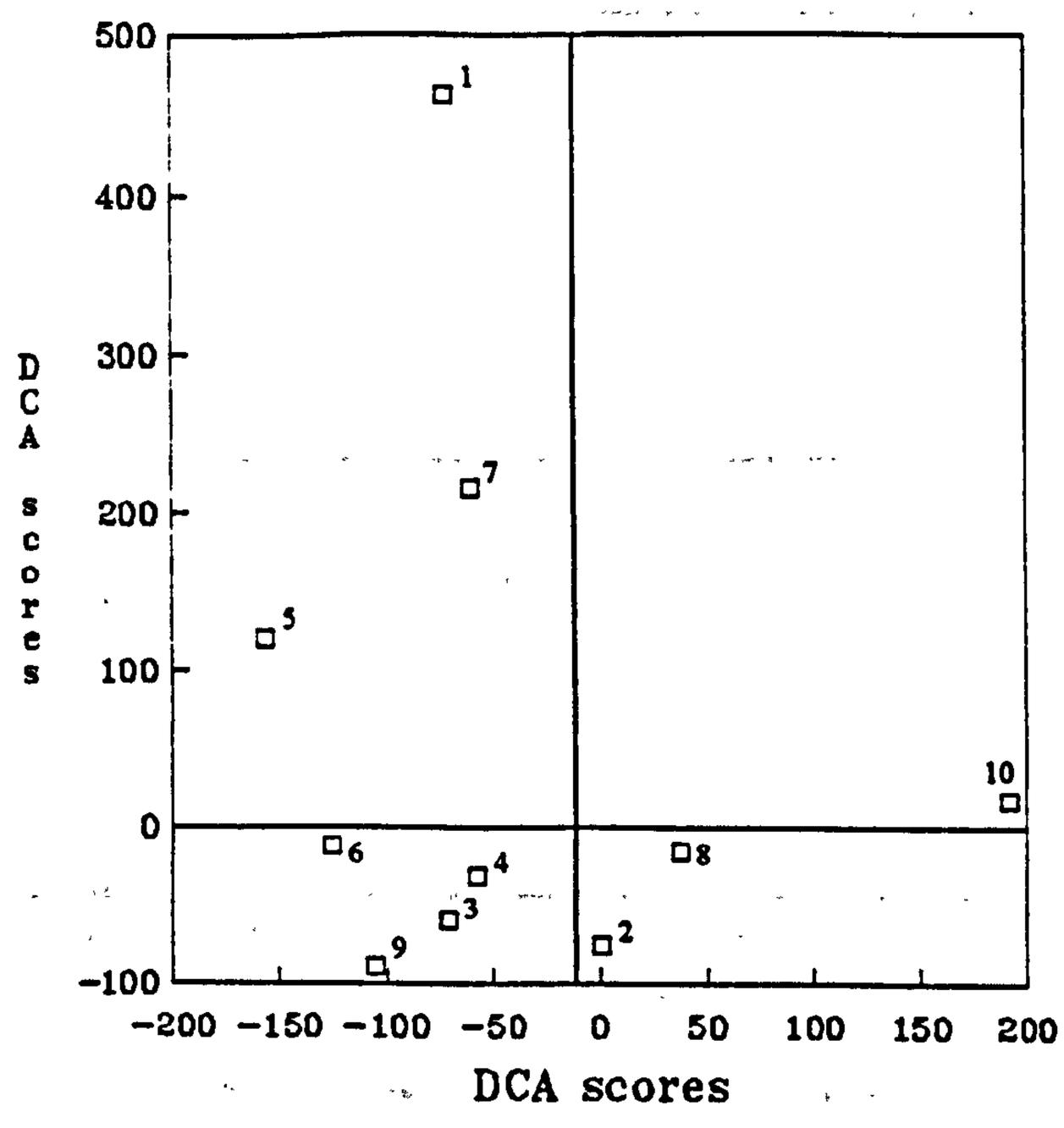
Before running the second stage of the analysis, Canonical Correspondence Analysis (CCA), seven variables were dropped as a result of the analysis of Variable Inflation Factors, leaving the remaining 13 as the basic input for the CCA analysis itself. The variables removed (see Table 3.11) were: cover by herbs, rush and litter; total cover and height of undergrowth; density of cones and of Sitka spruce saplings. Among the most

Figure 3.4. Detrended Correspondence Analysis (DCA) diagram showing the ordination of the fifteen sites according to the ten plant cover variables. Sites corresponding to different successional stages are represented by different symbols. DCA scores for each site are shown under the diagram (see text, Section 3.3.5).



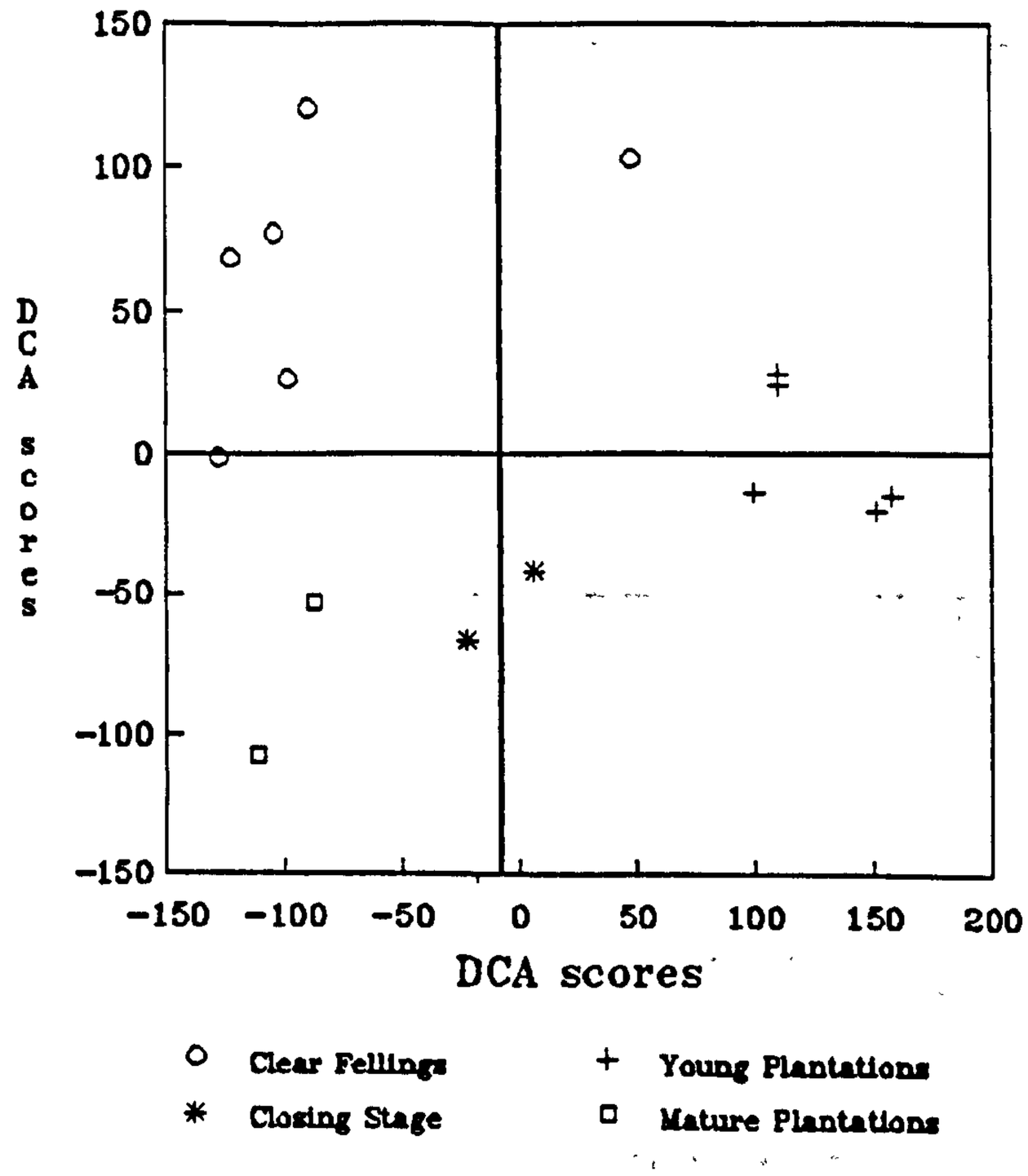
Sites	DCA scores	
	Axis 1	Axis 2
1) Corner 1	101	-16
2) Corner 2	127	-13
3) Corner 3	42	-31
4) Farm Felled	65	-14
5) Corner South	46	-19
6) View	-5	-40
7) Scots Pine	-37	-20
8) Road	-27	12
9) Adder	-5	-28
10) Stuart	-15	-24
11) Farm Young	-15	-24
12) Low Closing	9	95
13) High Closing	-22	63
14) Corner North	191	9
15) Corner Mature	169	8

Figure 3.5. DCA diagram showing the ordination of the ten plant cover variables according to the fifteen sites. DCA scores for each variable are shown under the diagram; variable numbers correspond to those in Table 3.11.



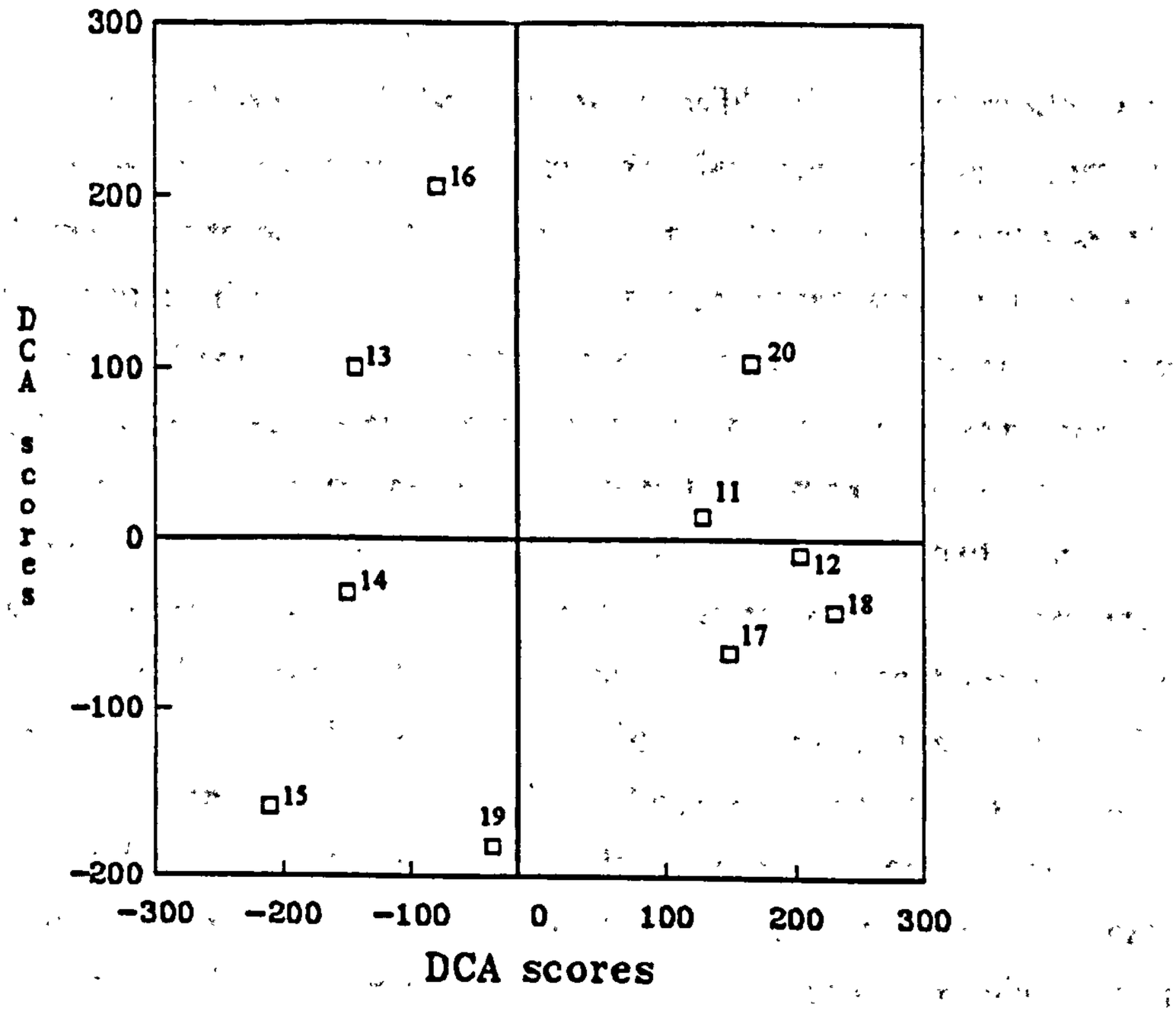
Plant cover variables	DCA scores	
	Axis 1	Axis 2
1) *Molinia caerula*	-72	461
2) Palatable grasses	0	-76
3) *Deschampsia flexuosa*	-71	-60
4) Heather	-58	-31
5) Bracken	-157	119
6) Bramble	-126	-12
7) Bilberry	-60	216
8) Herbs	37	-15
9) Rush	-106	-89
10) Mosses	191	18

Figure 3.6. DCA diagram showing the ordination of the fifteen sites according to the ten structural variables. Symbols as in Figure 3.4. DCA scores for each site are shown under the diagram.



Sites	DCA scores	
	Axis 1	Axis 2
1) Corner 1	-128	-2
2) Corner 2	-123	68
3) Corner 3	-105	77
4) Farm Felled	-90	120
5) Corner South	-99	26
6) View	48	102
7) Scots Pine	151	-21
8) Road	110	24
9) Adder	158	-15
10) Stuart	110	28
11) Farm Young	100	-14
12) Low Closing	-23	-67
13) High Closing	6	-42
14) Corner North	-112	-108
15) Corner Mature	-88	-54

Figure 3.7. DCA diagram showing the ordination of the ten structural variables according to the fifteen sites. DCA scores for each variable are shown under the diagram; variable numbers correspond to those in Table 3.11.



Structural variables	DCA scores	
	Axis 1	Axis 2
11) Height of undergrowth	127	13
12) Cover by undergrowth	202	0
13) Cover by bare soil	-144	100
14) Cover by litter	-151	-33
15) Density of Sitka cones	-211	-159
16) Cover by brashings	-81	205
17) Density of Sitka trees	147	-68
18) Density of broadleaved	229	-43
19) Density of low branches	-18	-181
20) Density Sitka saplings	165	103

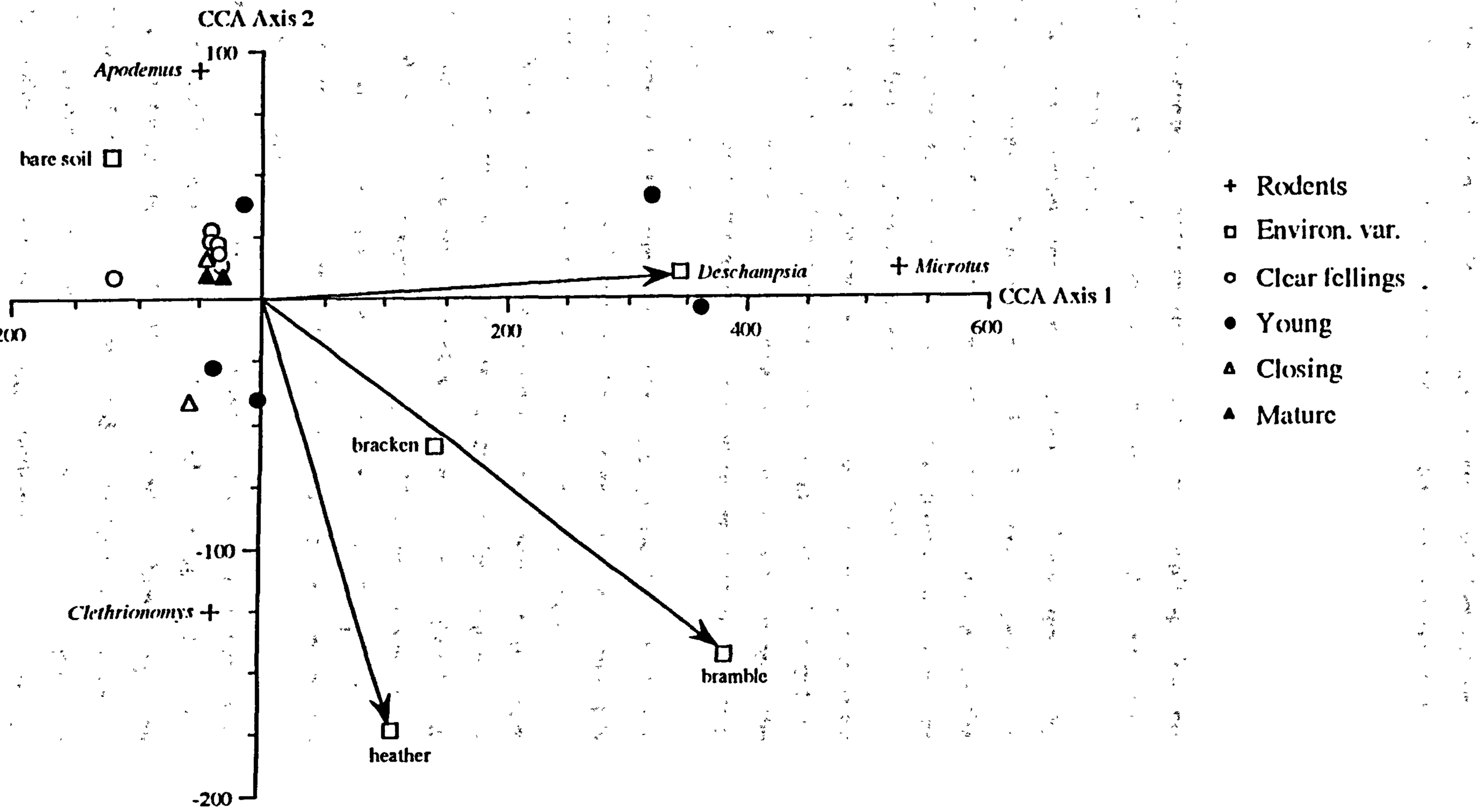
conspicuous losses were total cover and height of undergrowth, two potentially very important structural variables, but which could not be kept because of being correlated with several other variables. The variable kept in the analysis which showed the highest correlation with these structural variables was cover by heather ($r = 0.83$ and 0.66, respectively; both, $p < 0.01$). Therefore in the analysis that follows heather, to a certain extent, represents total cover and height of undergrowth.

CCA analysis was carried out until the simplest possible significant model was identified, in which five habitat variables (*Deschampsia flexuosa*, heather, bramble, bracken and bare soil) were left to account for the variation in the three rodent species. The first canonical axis accounted for 91.1 % of the variance represented in a species-environmental variables biplot based on the first two axes (Figure 3.8). The sum of the canonical eigenvalues, which indicates the proportion of community variation explained by the CCA axes, was 0.684. A Monte Carlo simulation showed the first axis to be significant ($p = 0.02$, 100 random permutations). Only three of the variables, however, had significant regression coefficients in relation to the first CCA axis: *Deschampsia*, $t = 6.13$; heather, $t = 8.17$; bramble, $t = 9.34$; all three, $p < 0.001$. Only these three significant variables are represented by arrows in Figure 3.8. Regression coefficients were not significant for bracken and bare soil ($t = 0.28$ and $t = 0.14$ respectively; both $p > 0.50$). Curiously, in an alternative model with *Deschampsia*, heather and bramble alone, no regression coefficient was significant. Bracken and bare soil, even though they did not have significant regression coefficients by themselves, were necessary to achieve a model in which other variables did.

Further examination of the CCA biplot suggests that the first axis can be related to a soil fertility gradient. High values along the first axis were achieved by bramble (a plant which is dependent on good soils) and the two young plantations which have good brown gley / brown earth soils: Road and Scots Pine (which lie on either side of *Deschampsia* in the biplot). At the other extreme of the first axis is bare soil. The second axis can be related to a shelter gradient, from bare soil to heather, a plant which provides good cover and, as mentioned above, was highly correlated with the estimates of total cover.

Among the rodent species, *Apodemus sylvaticus* was most closely associated to bare soil (although this was a non-significant environmental variable in the biplot) and to clear-fellings among the sites. However, all sites of all stages, except for Road and Scots Pine mentioned above, were close to the position of woodmice in the biplot, and to the position of *Clethrionomys glareolus* as well. This latter species was found in closest association with heather (along both axes), with bramble (along axis two) and to a lesser extent with bracken. *Microtus agrestis* was found in closest association with *Deschampia*

Figure 3.8. Canonical Correspondence Analysis diagram showing the ordination of sites, environmental variables and the three rodent species. Arrows indicate significant environmental variables (see text).



flexuosa (along both axes) and with bramble (along axis one, the proposed "fertility" axis). Among sites, its position was close to Road and Scots Pine only, a pattern opposite to the other two rodent species.

3.4 - Discussion

3.4.1 - Overall pattern of successional changes in the rodent communities - Pooling

all replicates of each stage, a pattern of successional change in rodent communities emerged which can be described as follows.

1) Mature plantations held two-species communities where woodmice tend to be numerically dominant, but bank voles are found in considerable abundance. Therefore the two dominant rodent species in mature Sitka spruce plantations at Hamsterley are the same two which are typically dominant in deciduous woodlands all around Britain, except in the restricted areas where *Apodemus flavicollis* occurs (Gurnell, 1985).

2) Recent clear-fellings had a similar pattern, the ratio of bank voles to woodmice being just slightly, and non-significantly, smaller than in mature plantations. This pattern suggests that communities in the clear-fellings were little more than a continuation of the communities present before the felling took place. Field voles were very rare in this stage: only one was ever caught in 2,205 trap nights.

3) In the young plantation stage, with its luxuriant ground vegetation (see Table 3.11), the communities changed completely. The third species (field voles) became numerically important in the community, while bank voles became as abundant as woodmice.

4) Some insight into what happens when the canopy starts to close was obtained from Burrows' (1991) study. His data included just two replicates, and therefore must be interpreted with care. However, they suggest that bank voles were still very abundant at this stage but almost all field voles had disappeared, although 1991 was an year when appreciable numbers of field voles were found elsewhere at Hamsterley. The pattern for the "closing" stage, as one would expect, represented a transition between the patterns found in young and mature plantations.

Few previous studies of rodent communities in British Sitka spruce plantations provide results strictly comparable to mine. Gibson's (1989) and Burrows' (1991) results were discussed above. In spring-summer 1990, Vadher trapped in Hamsterley three replicates of each of the same three successional stages I studied and his results on species compositions (Vadher, 1990) were consistent with mine. Thomson (1986) studied a Sitka spruce plantation in North Wales and found bank voles and woodmice as dominant species

in the mature stands but, in sharp contrast with my results, field voles were the the most abundant species in recent clear-fellings. As he did not provide a detailed habitat description it is impossible to know whether his clear-fellings (unlike mine) were quickly invaded by grasses - which could explain the observed difference (see Section 3.4.5).

The results of the present study are to some extent similar to findings of some single-site studies in conifer successional mosaics in Britain and continental Europe. Sharp and Wilson (1987) studied rodent populations in an area replanted with Scots Pine (*Pinus sylvestris*) in Yorkshire, where woodmice were dominant for the first three years after felling, bank voles increased thereafter and remained abundant through the young plantation stage until the end of the study (thirteen years after replanting) and field voles had a short-lived "pulse" of abundance between the fourth and the sixth year. All their findings were consistent with the pattern I found at Hamsterley. Ferns (1979a, 1979b), working in a japanese larch (*Larix kaempferi*) plantation in Devon, found that *M. agrestis* was very abundant in young (3-5 years old) plantations, but disappeared completely in the relatively short interval up to the "closing" stage (in his case when plantations were around 8 years old). Larch is a deciduous conifer, but nevertheless the undergrowth is sparse under mature stands, because in Winter little light is available to the ground vegetation anyway. As Ferns trapped just one site and his trapping was interrupted for three years (from the fifth to the eight year of the plantation), it is not clear to what extent cyclicity of the field vole population may have influenced his results. However, Venables and Venables (1965, 1971) also reported a sudden (rather than gradual) decrease of field voles linked with the closing of the canopy at a mixed Corsican-Lodgepole-Jack Pine plantation in Wales.

While some aspects of the successional pattern are consistent over a broad range of conditions (e.g. in conifer forests *M. agrestis* is nearly always restricted to young plantations; Hansson, 1971, 1974, Charles, 1981, Jensen, 1984, Staines, 1986), in other aspects similarities weaken as the geographic and taxonomic distances increase. For example, *Clethrionomys glareolus* is usually dominant over *Apodemus* spp in mature forests of those conifer species which allow the permanence of dense undergrowth; such as those studied by Hansson (1978) and Wolk and Wolk (1982) in North Sweden and Poland respectively.

Kirkland (1990) reviewed several studies of the effects of clear-fellings on small mammal communities in North America and in most cases found increases in both in diversities and in population densities. Neither of these effects were detected in Hamsterley by the present study. Increases in diversity are hindered in Hamsterley by the restricted pool of small rodent species available in the North of England. The only

abundant species that could be added to the mature woodland community, *Microtus agrestis*, does not colonize unless a continuous layer of grasses develops (Section 3.4.5). In this situation of absence of specialists, the most generalist, adaptable species is likely to reap most of the benefits of the new resources available in clear-fellings and to become dominant there. That was the pattern found by Morrison and Anthony (1989) in Oregon, the dominant species being the generalist white-footed mouse *Peromyscus maniculatus*. In the present study woodmouse was the dominant rodent on most sites and occasions, and the actual extent of its dominance tends to be underestimated by the pooling of data (see next Section).

Overall rodent densities were not significantly different between any successional stages, despite young stages of spruce forests having much higher productivity than older stages (Hansson, 1974). Due to its grazing diet, field vole is the species which benefits most from the increase in production and when that happens they can be found in very high densities in young plantations (e.g. Hansson, 1971, 1974; Charles, 1981). However, field voles were not always present in young plantations at Hamsterley, and abundances of all species were highly variable both in time and space within each stage (see Sections 3.4.2, 3.4.4 and 3.4.5). Both factors contribute to the finding that no stage had total rodent densities consistently higher than other stages.

3.4.2 - Spatial scales of variation in the rodent communities - If instead of pooling sites as in the previous Section we analyse the data on a site-by-site basis, the picture sketched above is incomplete in at least two points, as a second look at Table 3.3 will show.

First, bank voles were much less abundant than woodmice in clear-fellings in every case except at two sites in Summer 1992. These were Corner South (where the first bank vole caught there was the only individual present) and Corner 2 (where bank voles outnumbered woodmice tenfold). In this trapping session at Corner 2 alone two thirds of all bank voles found in all clear-fellings in the restricted data set were recorded. Indeed, the data from Corner 2 in Summer 1992 alone accounted for the failure to find a significant difference between the proportion of bank voles to woodmice in clear-fellings and mature plantations (chi-square removing Corner 2 Summer 92: using restricted data set, $X^2 = 8.10$; using total data, $X^2 = 9.82$; either, $p < 0.01$). Therefore, the pattern for clear-fellings may be better described by saying that woodmice are usually dominant (much more so than in mature plantations) and bank voles are usually rare, but exceptionally this pattern can be dramatically reversed. Possible reasons leading to the unusual pattern in Corner 2 in Summer 1992 will be discussed in Chapter 5.

The second point similarly shows pooling of sites hiding smaller scale heterogeneity. The pooled pattern in young plantations is three species with similar abundances. However, of the five young plantations trapped regularly, two were consistently dominated by woodmice (Adder and Stuart), one by bank voles (Farm Young) and two by field voles when they were abundant in Hamsterley as a whole, and by woodmice when field voles were absent (Road and Scots Pine). Thus the three-species community found for the young plantation stage as a whole was seldom found at any given specific site.

Similar findings of different patterns at different spatial scales were reflected in the diversity and evenness indices as well (see Section 3.3.4). With all sites of each stage pooled, diversity was highest in young plantations, as a straightforward consequence of the additional species plus the most even abundances found in this stage. Mature plantations and clear-fellings had diversities similar to each other, but lower than young plantations. When instead of pooled the sites were averaged, diversity at mature sites was on average as high as in young plantations, while clear-fellings were significantly less diverse than either of the two. When the evenness component is analised separately, the pattern becomes more clear. As expected from Figure 3.3, with pooled sites young plantations had the highest evenness, followed by mature plantations and clear-fellings in this order. However, in a site by site basis, average evenness was at least as high in mature sites as in young plantations, with clear-fellings again coming last.

When seen together, these results suggest that young plantations are more diverse than mature forests because of an inter-site component (β, or differentiation, diversity - Magurran, 1988) rather than by within-site diversity (α, or point, diversity - Magurran, 1988). Differentiation diversity is a result of species replacement: on average, young sites had neither more species nor more even abundances than mature sites; but in young plantations different combinations of species were found at different sites.

3.4.3 - Temporal variation versus spatial variation - In addition to the spatial variation, a considerable amount of temporal variation was found. ANOVA (Table 3.6) showed that in the four years of the study both woodmice and field vole abundance differed significantly.

For woodmice, marked non-cyclic year to year fluctuations in abundance are often found, due, for example, to varying seed supplies (Gurnell, 1981). Within mature plantations numbers of woodmice were much higher in 1991 than in the other years. This probably was due to 1991 being an excellent seed year in Hamsterley (see Chapter 4). In the case of field voles, the interannual variation found was probably associated with a

"cyclic" population fluctuation. *Microtus agrestis* was found in high numbers in Road and Scots Pine and was present in two other grids in 1989, a year which could have been the peak of the cycle. This was followed by a crash: by Summer 1990 the species had all but disappeared from all sites. A slow recovery was apparent through 1991 (see also Chapter 4) and 1992, although a second peak had not yet been reached by the end of this study. It is well known that *Microtus agrestis* populations follow a 3-4 year cycle throughout most of the distribution of this species (Elton, 1942; Chitty, 1952; Myers and Krebs, 1974; Marcstrom *et al.*, 1990), although some populations in Britain (Richards, 1981, 1985) and Southern Fennoscandia (Erlinge *et al.*, 1983; Hansson, 1984; Erlinge, 1987) do not show regular fluctuations.

At first sight, inter-site variation seems to be smaller than interannual variation: Kruskal-Wallis or Mann Whitney tests showed significant inter-site differences only for bank voles at mature forests. However, in four out of six non-significant tests (young plantations for each of the species, and clear-fellings for bank voles) a value corresponding to $p < 0.10$ was found (Table 3.6). Non-parametric tests were used because the data set did not meet the criteria for use of their parametric analogues (Section 3.2.2), but the former have less power (Zar, 1984). Therefore it seems that inter-site variation may have been underestimated by the tests used.

Both ANOVA and Kruskal-Wallis compare among-groups variation (AG) with within-group variation (WG). Inter-site variation was WG when comparing years, and conversely interannual variation was WG when comparing sites. Thus these two analyses can be seen as reciprocal to each other. Therefore it is not surprising that interannual differences could be demonstrated for woodmice which showed the least inter-site variation, and inter-site differences could be demonstrated only for bank voles which showed the least interannual variation. Field voles showed great variation both in time and space. It is perhaps surprising that significant interannual variation could be demonstrated even in the presence of such high inter-site variation, and conversely that for young plantations inter-site variation was nearly significant (see previous paragraph) in spite of the high interannual variation.

In overview, each species has a distinct, characteristic place in a plane defined by population variation along two axes: time and space. Woodmice, the most habitat generalist of the three species, shows little spatial variation but considerable interannual variation. Bank voles, much more of a habitat specialist than woodmice, present more inter-site variation but have more constant populations. Field voles populations present very high variation both in space and in time. These patterns are roughly consistent with previous ideas on habitat use (Gurnell, 1985) and population fluctuations (Richards, 1981;

Alibhai and Gipps, 1985; Flowerdew, 1985) of the species concerned, although it must be emphasized that cyclicity and intensity of fluctuations in both voles vary considerably accross their distributions (Alibhai and Gipps, 1985; Hansson and Henttonen, 1985; Marcstrom *et al.*, 1990).

3.4.4 Competition between Woodmice and Field Voles ? - The woodmouse *Apodemus sylvaticus* was the most ubiquitous species in the present study. It was found in all sites and often in moderate to high densities; in only five trapping sessions were no woodmice caught. Therefore they were conspicuous by their almost complete absence in the three trapping sessions where highest numbers of field voles were captured (Road, Summer 1989 and Summer 1992; Scots Pine, Summer, 1989). In these same two sites, woodmice were the dominant species in 1990 and 1991 when *Microtus agrestis* in turn was almost absent. In clear-fellings, just one field vole was captured in the whole study period - coincidentally or not, on another of the rare occasions when woodmice were absent. This pattern accounts for the significant negative correlation found between the abundances of those two species (Section 3.3.3).

A negative interaction between *M. agrestis* and *Clethrionomys glareolus* has been found in several studies in Scandinavia (Myllymaki, 1977a; Hansson, 1979, 1982, 1983), where bank voles tend to be excluded from grassland when numbers of field voles are high, but the two species coexist when densities of *M. agrestis* are low. Flowerdew *et al.* (1977) suggested that the reverse pattern could be occurring between the two species in fenland in Cambridgeshire, where bank voles seemed to affect the distribution of field voles. Competition between field voles and woodmice has not often been proposed, although a pattern very similar to the one I found in Hamsterley was described by Brown (1954:166-8) in Silwood Park, Berkshire. The pattern I found suggests that woodmice and field voles in Hamsterley interact in a way similar to the interaction of the two voles described above. The hypothesis is that *M. agrestis* (a grass specialist) would be the superior competitor which, when in high densities, can exclude *A sylvaticus* (an habitat generalist) from productive grassy sites in fertile soil (see Sections 3.4.5 and 3.4.6). However, *A. sylvaticus* can opportunistically invade when the numbers of field voles are low during the low stage of their population cycle.

The above hypothesis of asimmetric competition is consistent with the data gathered so far at Hamsterley, although the evidence in its support is just correlative and therefore does not exclude alternative explanations. For example, conceivably the species could have highly distinct habitat preferences, and subtle habitat changes in time could make the habitat favorable sometimes for one and sometimes for the other. This

explanation does not seem likely if one takes into account how generalist woodmice are in habitat use (e.g., Gurnell, 1985). The hypothesis of asimmetric competition could best be tested using an experimental approach. Field experiments involving selective removal of one species have often been useful to examine interspecific interactions in small mammals (e.g. Grant, 1972; Gliwicz, 1981; Montgomery, 1981; Brown *et al.*, 1986; Schoener, 1983, 1986). However, the most promising field experiment was unfeasible during the time available for my fieldwork. It would have involved the removal of *M. agrestis* (the species hypothesized to be competitively superior) and subsequent monitoring of possible changes in numbers or habitat use by *A. sylvaticus* (the species hypothesized to be competitively inferior). To perform this experiment, considerable numbers of *M. agrestis* would need to be removed (otherwise the effect on *A. sylvaticus* would be negligible), but this was not feasible because populations of field voles had not yet reached a peak in Hamsterley by the end of this study in June 1992. It would be highly desirable to perform this experiment at a future time when high densities of *M. agrestis* can again be found.

3.4.5 - Habitat changes and the related changes in the rodent communities - The patterns outlined in the previous Sections suggest that young plantations are the most unpredictable stage of succession for rodent communities in Sitka spruce, both in terms of species composition and relative abundances. By unpredictable I mean that a local rodent community cannot be accurately predicted by the age of the plantation alone in the case of young plantations, while such a prediction is much more likely to be accurate for a clear-felling or a mature plantation. Rodent community succession begins with the usually stereotyped composition in clear-fellings, then it can follow nearly any path during the young plantation stage, but gradually it moves again towards a more predictable outcome as plantations reach maturity.

But how does the "unpredictability" of rodent communities in the young plantations arise ? According to Gurnell (1985), quantity and species composition of the ground vegetation holds the key to small mammal community structure in planted forests. The ground vegetation found in each plantation is in turn affected by soil characteristics, seed bank and colonization history (Hill, 1979b, 1986). To explain the high variation among local communities in the young plantation stage, one has first to show evidence that there is higher variation in the vegetation of young plantations than in the other stages, and that such variation favours several distinct rodent communities.

Results of DCA analysis, either by vegetation or structure (Figures 3.4 and 3.6) do not seem to provide such evidence. Young plantation sites are as clumped in the diagrams

as any other successional stage. However, a more careful interpretation suggests that sites are clumped due to the large gaps between stages in several variables. For example, most variables of plant cover have high values in young plantations, and zero values in mature Sitka. Conversely, densities of low branches, for example, are high in "closing" and mature plantations, very low in most young plantations, zero in clear-fellings (Table 3.11). The ordination pattern reflects chiefly those all-or-nothing variables, that is, exactly the ones which change with succession in most predictable ways (see species scores under Figures 3.5 and 3.7). Therefore the effect of such variables dwarfs other variables which show more subtle within-stage variation - as happens with most plant cover variables within young plantations (Table 3.11).

When the rodents are brought into the picture by CCA (Figure 3.8) those previously hidden differences become apparent. For example, there is an isolated cluster at the right of the biplot formed by three kinds of entities: two young plantation sites (which are Road and Scots Pine), one habitat variable (the grass *Deschampsia flexuosa*) and one rodent species (*Microtus agrestis*). Field voles are also associated with bramble, along axis one. Road and Scots Pine were the sites with highest abundance of field voles (Sections 3.4.2-3.4.4). The reason for the association between field voles and the wavy hair grass *D. flexuosa* is not immediately clear: this grass is considered unpalatable to field voles (Ferns, 1976). One would expect field voles to be more closely associated to the variable "palatable grasses" instead, as Ferns found that *Holcus lanatus* and especially *Agrostis* spp are important food resources to *Microtus agrestis*. Palatable grasses were excluded from the final CCA model precisely because they had a high correlation with *D. flexuosa*, and models using this last variable explained better the variation in rodent communities. This puzzling result seems to be due to palatable grasses occurring more often than *D. flexuosa* in sites were field voles were not present. Palatable grasses were present in all five *M. agrestis* sites (and abundant in Road and Scots Pine), but they were found in eight other sites as well. *D. flexuosa* was also present in all *M. agrestis* sites, but in only four others (Table 3.11). The presence of palatable grasses is a necessary but not a sufficient factor to explain the occurrence of field voles, which need continuous ground cover by grasses (Ferns, 1976, 1979b; Hansson, 1977). A sparse cover even of the most edible grasses is not enough. *D. flexuosa*, abundant in Road and Scots Pine (and paradoxically contributing to good ground cover there), but with a distribution more restricted than palatable grasses and therefore more similar to the voles' own distribution, seems to be in a sense representing palatable grasses in the CCA model.

Bank voles were found in all young plantations, but they were consistently dominant only in the Farm Young site. The unique composition of the rodent community

at this site was matched by an unique plant community as well. Farm Young was the site where Sitka spruce was found in by far the highest density (mostly due to self-seeding rather than planting) and also the site with highest abundance of heather, which was the variable most closely associated with bank voles in CCA analysis (Figure 3.8). Farm Young was also the young plantation with lowest overall abundance of grasses and it showed a relatively high abundance of bramble, which was also found to be associated to bank voles in the CCA biplot (Figure 3.8).

An association between bank voles and bramble has been reported previously by Southern and Lowe (1968) and Gurnell (1985:388). Brambles provide edible berries which may be a good food resource for bank voles; Hansson (1985:151) found berries to be an important food source for bank voles in conifer forests and reforestations in Scandinavia. Heather, on the other hand, is not likely to be a good food source for bank voles. Its seeds are very small and difficult to gather. Only the current year shoots and flowers, at the exposed top of the plant, are available to herbivores, while the bulk of the biomass, the woody part, is not (Miller, 1979). Those factors probably explain why heather does not appear usually in the diet of voles (Hansson, 1985). However, heather does provide good cover and indeed it showed a very high correlation with the total amount of ground cover (Section 3.3.4). The position of bank voles in relation to the second CCA axis in Fig. 3.8, which seems to represent a cover gradient (Section 3.3.5), is indicative of their strong preference for good cover. Several other studies have shown bank voles to be associated with dense ground cover (Fullagar *et al.*, 1963; Kikkawa, 1964; Jewell, 1966, Ashby, 1967; Flowerdew *et al.*, 1977; Montgomery, 1979; Mazurkiewicz, 1991), probably because of protection against aerial predators (Southern and Lowe, 1968; Southern, 1970). Actually *C. glareolus* has more often been associated with bracken than heather (Evans, 1942; Fullagar *et al.*, 1963, Jewell, 1966). Bracken was indeed a component of the CCA model, but it was not significantly related to the first axis, and its association with bank voles was slightly less than heather's (Figure 3.8). Healing *et al.* (1983) argued that what is preferred by bank voles is dense cover with little understorey so that there are open spaces under the cover through which voles can move. In their study area (Skomer Island) they found that sparse bracken with an undercover of grass (a situation similar to the Road and Scots Pine sites) was a bad habitat for bank voles, while there was a trend (non-significant) for association between bank voles and heather. Dense heather can provide the structural conditions needed for bank voles: a closed ground cover with plenty of open space underneath. In the case of Farm Young, cover was further increased by the exceptionally high density of young spruce trees, which resulted in a density of low branches five times higher than at any other young plantation

(Table 3.11). Put together with the heather, this makes Farm Young a dense thicket with few exposed patches, therefore fulfilling bank voles' cover requirements well. Again, unsuitable food plant(s) were found to have a structural role which is necessary to explain the abundance of the vole species.

Abundance of *Apodemus sylvaticus* in young plantations was less variable than the abundance of voles: woodmice were at least moderately abundant in all sites of that stage, except when field voles were numerous (previous Section). In the two sites where woodmice were consistently dominant (Adder and Stuart) their abundance was not exceptionally high, but voles were seldom found (see Table 3.3). Examination of the CCA biplot does little to clarify woodmice's habitat preferences: they were closely associated only with the amount of bare soil, which seems to reflect woodmice dominance in clear-fellings rather than fine habitat preferences within young plantations. The most abundant grass at Adder and Stuart sites is *Holcus mollis* - which, contrary to *H. lanatus*, produces very low, prostrate tussocks under which field voles cannot make their tunnels, and which would not provide good cover for bank voles (see discussion above in this Section). Dense patches of heather are found at the two sites, but the low density of trees does not create a ground cover for bank voles as good as in Farm Young. Good food sources may be fewer as well: bramble, for example, is scarce (Table 3.11). Given that the specific habitat factors which allow dominance by either vole in the remaining three sites are not found at Adder and Stuart, and that woodmice in general are more habitat generalist than the voles (Sections 3.4.1, 3.4.3; Gurnell, 1985), it seems that at Adder and Stuart woodmice are dominant "by default", in the absence of the circumstances that favour either vole.

3.4.6 - An overview: soil characteristics, vegetation, and the heterogeneity of each successional stage - In all five young plantations discussed above, vegetation seems to be determined to a great extent by local characteristics of the soil. For example, the association of field voles with bramble may reflect good soils: bramble is usually found on fertile soils (Hill, 1979b). Indeed, Road and Scots Pine sites have mostly nutrient-rich, well-drained brown gley/brown earth soils (Table 3.1) which allow a high productivity, indeed the highest overall abundance, of grasses (Table 3.11). *Deschampsia flexuosa* is likely to be especially favoured by the conditions at those sites, due to its preference for well-drained soils (Gibson, 1989).

The soils in both woodmice dominated sites, Adder and Stuart, are surface-water gleys. These can be good soils as far as mineral nutrients are concerned, but they are water-logged which makes them unfavourable to many plants which demand well-drained

soils. Such plants include *D. flexuosa*, bramble and bilberry, which are scarce at Adder and Stuart (Table 3.11).

In Farm Young site, the soil is mostly podzolic (either podzolic gley or typical podzol), quite unlike the soil in any other young plantation within the restricted data set - but rather similar to Corner Young, where bank voles were also found in high abundance (Table 3.3). As discussed in Chapter 1, podzolic soils are highly acidic - indeed, Vadher (1990) found an average pH of 3.69 at Farm Young site - and the superficial and intermediate horizons are poor in nutrients. Such conditions favour plants which are tolerant to acidic conditions, while having relatively deep root systems in order to reach the nutrients available under the podzol. Both requirements are fulfilled by heather and Sitka, plus some highly adaptable herbs as the rosebay willowherb *Chamaenerium angustifolium* (the most abundant herb in Farm Young), but not by grasses. Reasons for the relatively high abundance of bramble, normally found on good soils, are unclear. Farm Young is adjacent to Pennington Farm where bramble is found in abundance growing along pasture edges and verges. When such an abundant source of colonizers is available, bramble may spread vegetatively to areas to which is not especially well suited, and the absence of grasses may also help it to thrive in Farm Young (J.A. Pearson and G. Simpson, pers. comm.).

Soil characteristics interact with colonization history and seed banks in determining the vegetation found at any given site. In some cases the influence of these latter factors can be considerable. The case of bramble in Farm Young has just been mentioned. Bracken is almost totally dependent on vegetative spread (Hill, 1986) and it will not invade a newly opened habitat unless a suitable source of colonizers is available at a short distance; therefore soil characteristics alone cannot explain its distribution well. Heather is not usually a dominant plant in first rotation young conifer plantations, and the fact that it is sometimes dominant in second rotation may be partially explained by its good survival as seeds in soil, allowing it to be more abundant and viable than most competitors in seed banks when the first rotation is felled (Hill, 1979b, 1986). However, the suitability or not of the soil for grasses may play a part as well, not least because some grasses (like *Agrostis canina*) also survive for long periods in the seed bank (Hill, 1979b). The importance of seed banks and particularities of colonization history must not be underestimated. Nonetheless, soil is an essential limiting factor for plant communities in young plantations and an understanding of its variations helps considerably to make this "unpredictable" stage more predictable.

As an overview, the following conceptual model is suggested to explain the interplay of spatial and successional variations in rodent communities in Sitka spruce

plantations at Hamsterley. The high β-diversity of rodent communities in young second-rotation plantations arises because the marked local differences in soil characteristics result in different associations of ground vegetation which in turn make each site most suitable for a different rodent species, through the mechanisms discussed in this and the previous Sections. Soil types under mature plantations in Hamsterley are as varied as under young plantations, but this variation is "buffered" as the ground vegetation, whatever its identity, gets shadowed out. The habitats at the various sites change gradually towards similar communities: single tree stands, bare ground except for mosses, Sitka seeds as the main food resource. When trees are clear-felled, inter-site variation is small at first but tends to increase as ground vegetation develops and soil differences once again are expressed.

CHAPTER 4

RODENT POPULATIONS IN A HABITAT MOSAIC PRODUCED BY FELLING: I: POPULATION DYNAMICS IN THE MOSAIC AS A WHOLE

4.1 - Introduction

4.1.1 - Rodent populations in an habitat mosaic: scales of analysis - There has been considerable interest recently in the responses of small mammal populations to habitat heterogeneity (e.g. Geuse *et al.*, 1985, Dickman and Doncaster, 1987, 1989, Bauchau and Le Boulengé, 1991, Montgomery *et al.*, 1991, Szacki and Liro, 1991, Zhang and Usher, 1991; see Chapter 1). The present Chapter and following two report the results of a Capture-Mark-Recapture study of rodent populations within an habitat mosaic (hereafter called "Corner Complex") produced by the felling of a block of mature Sitka spruce in Hamsterley Forest. Corner Complex was heterogeneous both spatially (at any given time during the study there were both mature plantations and clear-fellings within the area) and temporally (because felling of the block took place during the study).

Small mammal populations within the habitat mosaic in Corner Complex were studied at two different spatial scales. At the coarser scale, population dynamics of each rodent species were analysed in the mosaic taken as a whole. Such analyses assumed that populations sampled in different grids were not isolated from each other, thus it should be possible to account for the temporal variation in numbers in Corner Complex as a whole, in spite of its habitat heterogeneity. Analyses at this level are discussed in the present Chapter.

At the finer scale, population processes were analysed in each individual grid separately. Analyses at this scale aimed to relate variations in spatial distribution within the rodent populations with two factors, which are discussed in separate Chapters although they are not likely to be independent. Chapter 5 discusses the effects of the spatial and temporal habitat heterogeneity brought about by felling on the spatial distribution of rodents. Chapter 6 relates the rodent population fluctuations, discussed in the present Chapter, to their spatial distribution.

4.1.2 - Aims of the study of rodent populations in the Corner Complex as a whole - The aims of the study reported in the present Chapter are as follows:

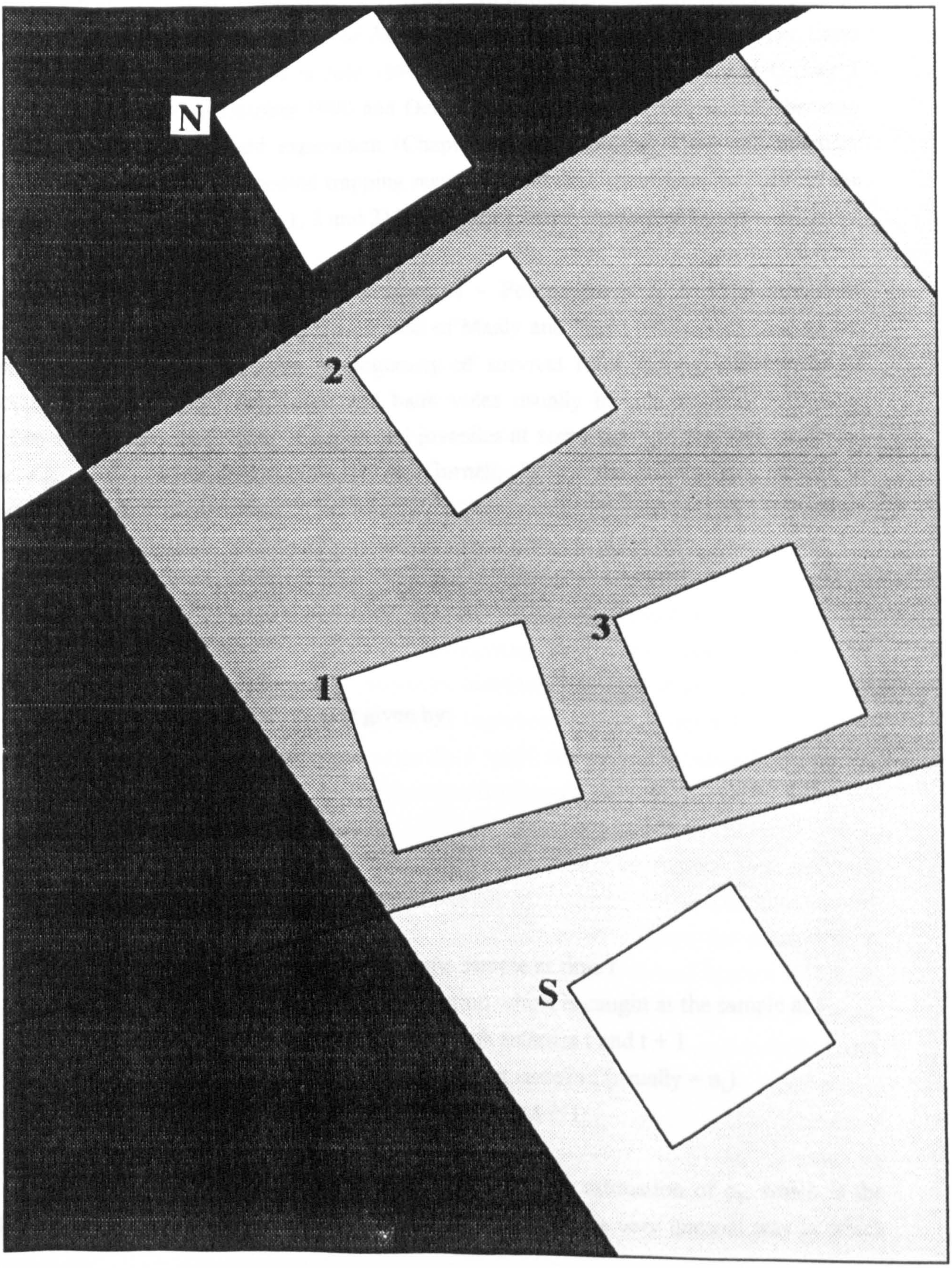
(1) To characterize the pattern of annual fluctuations in the rodent populations in Corner Complex, and to analyse the population dynamics of the most common species.
(2) To assess the validity of the assumption that rodent "populations" in different grids within Corner Complex are highly interconnected, through the analysis of patterns of use of space by individual rodents within the area.
(3) To estimate home range sizes and average distance moved between captures of individuals of each species and sex, to characterize seasonal variations in those parameters, and to relate them to the population dynamics studied under (1).
(4) To compare the population dynamics of the rodents in Corner Complex with those described for the same species in other habitats, highlighting the similarities and differences in the likely mechanisms.

4.2 - Methods

4.2.1 - The Corner Complex: trapping design and trapping programme - Within a Sitka spruce block of six hectares, scheduled for felling in summer 1990, four standard grids (Section 2.2) were trapped from May, 1990 onwards. Two grids (Corner 1 and Corner 2) were located within the block to be felled. Therefore, they were initially mature forest (planted in 1946) and became clear-fellings when their trees were cut and removed in July-August 1990 (see Chapter 5). The two other grids (Corner South and Corner North) were adjacent to the block being felled and therefore their successional stage did not change during the study. Corner North was a mature plantation (also planted in 1946) and Corner South an old (1989) clear-felling, which had not been replanted. A fifth grid (Corner 3) was added in September 1990 within the block that had just been felled. The positions of the five grids and habitat types within and around the Corner Complex are shown in Figure 4.1.

Year of planting and soil characteristics of each grid are presented in Table 3.1, Chapter 3. From Table 3.1 it can be seen that there were several soil types represented in Corner Complex, which is just one more example of the great spatial heterogeneity in soils in Hamsterley Forest (Chapters 1 and 3). Soils in the north of Corner Complex (including the entire grid Corner North and part of the grid Corner 2) and the extreme south (including part of Corner South) were peat covered by a *Calluna vulgaris* and *Eriophorum vaginatum* blanket bog. Most of the central part was a mixture of surface-water gley and podzolic gley, and an ironpan occupied part of Corner South.

FIGURE 4.1. Position of the five standard grids trapped within the Corner Complex. Within the mature plantation felled in July-August 1990, trapping started in grids 1 and 2 before felling, and in grid 3 in September 1990. Corner North (N) and Corner South (S) were respectively a mature plantation and a clear-felling throughout the study (May 1990-June 1992).



A standard trapping session (Section 2.2) was carried out monthly (except for January) in all grids from 1990 until March 1992. An additional standard trapping session was carried out in June 1992, as part of the Censuses (Chapter 3). However, Corner 1 and Corner 2 could not be trapped in July 1990, due to the felling. Corner 1 and Corner 3 could not be trapped in October 1990 and October-November 1991 respectively because of brash removal for a field experiment (Chapter 5). In December 1990 and February 1991, because deep snow hindered trapping sessions, valid data were obtained only for the new clear-felling grids (Corner 1, 2 and 3) but not for Corner North and South.

4.2.2 - Estimates of Population Parameters - Population size, survival and daily trappability were estimated using the method of Manly and Parr (1968). This method has the advantage of not assuming homogeneity of survival rates among individuals. As population dynamics of woodmice and bank voles usually include marked differences between survival probabilities of adults and juveniles at some times of the year (as found by e.g., Watts, 1969, Flowerdew, 1974, Gurnell, 1978), the Manly-Parr method is appropriate for these species.

The Manly-Parr estimate of population size at time t is given by

$$N_t = \frac{n_t}{p_t}$$

And the estimate of survival is given by:

$$S_t = \frac{a_t}{r_t.(p_t + 1)}$$

Where:

n_t = number of individuals caught at the sample at time t
p_t = estimated proportion of the population which is caught at the sample at t
a_t = number of individuals captured on both samples t and t + 1
r_t = number of marked individuals released at sample t (usually = n_t)
$p_t + 1$ = proportion of r_t which is recaptured at t + 1

The key stage of the Manly-Parr procedure is the estimation of p_t, which is the trappability estimate. This step, however, is dependent on the very unusual way in which

data are tabulated for this method and it cannot be easily explained without reference to a detailed example (Begon, 1979: 38). Therefore, for more details of the Manly-Parr procedure, the reader is refered to Begon (1979: 38-42) and Seber (1982: 233-7).

Population size estimates are likely to be negatively biased in months when less than five grids were trapped (listed in Section 4.2.1). Two cases were distinguished and treated differently, as follows.

(1) Months when only two grids were trapped (during felling) or three grids were trapped, missing Corner North and South, the grids at each extremity of Corner Complex. Such estimates were not considered representative of the whole population and thus they were not used when relating population sizes to any other parameters. However, estimates for those months are included (in parentheses) in the Tables below.

(2) Months when four grids were trapped, missing one of the central grids. In these months the negative bias was likely to be smaller than the 20% the reduction in number of grids would suggest, for two reasons. First, because of frequent inter-grid movements, individuals not caught in the grid missing in a particular month t might be caught elsewhere in the same month. Second, if they were not caught in month t but were recaptured subsequently, that would result in a lowered trappability estimate in month t and a correspondingly increased population size estimate. This would partly compensate for the missing grid. The precise correction factor could not be estimated from Manly-Parr formulae. Because of this, the correlations between population sizes and the other demographic parameters and spatial parameters (see next Sections) were tested using two alternative sets of population size estimates (a) uncorrected; (b) corrected by multiplying by 1.25 the values obtained in cases when four grids were trapped instead of five (as indicated above, this probably over-compensates for the reduction in the number of grids trapped).

All demographic parameters which can be density-dependent (e.g. survival, recruitment, reproductive rates) are likely to be related to population density (i.e. number of individuals per unit area) rather than to population size. However, the estimation of population density of small mammals is a complex problem. It is well known that small mammals often enter the grids from adjacent areas, so the actual sampling areas are larger than those covered by the grids. However, it is difficult to estimate the extent of this "edge effect". Several methods have been proposed to correct for edge effect (see Smith *et al.*, 1975, Flowerdew, 1976a, Tanaka 1980, Schroeder, 1981, Seber, 1982), yet actual sampling areas can seldom be estimated with great accuracy. Thus, instead of trying to estimate densities, I opted to correlate the remaining demographic parameters with my estimates of population sizes. Such analyses rely on the assumption that there is a high

correlation between population size and population density, so that the former parameter can be used as an index to the second.

For estimating survival of specific age classes instead of the whole population, sample sizes often were not enough for using the Manly-Parr procedures. Therefore the "minimum survival" method was used, following Chitty and Phipps (1966) and Montgomery (1980). Minimum survival (P_{min}) is given by

$$P_{min} = \frac{N_t}{N_{t-1}}$$

Where N_t is the number of individuals still alive in month t, out of N_{t-1} captured in the previous month. When calculating P_{min} for juvenile or subadults, individuals which had changed to the next age class by month t were included in N_t.

Per capita recruitment rates at time t were estimated simply as the number of new juvenile individuals appearing in the population between t -1 and t, divided by population size at t. Recruitment estimates were calculated using juveniles only, as recruitment of individuals of older age classes is difficult to separate from immigration and/or from individuals actually recruited before month t but not captured previously.

The proportion of reproductive females in month t was estimated as the number of females showing any signs of reproductive activity (see Chapter 2) divided by the number of subadult plus adult females captured in that month.

For each rodent species, correlations between population sizes, survival rates, recruitment rates and proportion of reproductive females were tested by means of Pearson's product-moment correlation coefficients. All possible pairwise correlations were tested, except the ones involving pairs which by definition are not independent (e.g. overall survival and survival of one age class). Additionally, delayed density-dependence of all survival, recruitment and reproductive rates was tested by correlating the values of these parameters in month t with population size estimates in the previous month. Data were normalised by either logarithm or arcsine transformations (Zar, 1984) when necessary.

In most cases the interval between trapping sessions was not exactly 30 days, but all survival, mortality and recruitment estimates were converted to 30 day rates - i.e rates expressing respectively survival, mortality and recruitment over a period of 30 days. This convertion was carried out using a logarithmic transformation, as follows (exemplified with a survival rate, S_t):

$$S_t = \frac{N_t}{N_{t-1}} = e^{s.d} \quad \therefore \quad s = \ln \frac{S_d}{d} \quad \text{and} \quad S_{30} = e^{30s}$$

Where:

S_t = survival rate estimate for the month t

N_t and N_{t-1} = numbers at month t and at the previous month respectively

s = daily survival rate

d = actual number of days separating the trapping sessions at t and t - 1

ln and e = natural logarithm and its base, respectively

S_{30} = 30 day survival rate

Body weights were used as the criterion to separate age classes. The weight chosen to separate juveniles from subadults was the one at which it became common to find individuals with signs of reproductive activity. Similar criteria for separation of age classes have been used in previous studies on British rodents (e.g., Flowerdew, 1974; Gurnell, 1978). The values actually used in the present study were: for *A. sylvaticus*, juveniles up to 15g, subadults, 16-20g; adults, 21g plus. For *C. glareolus*, the respective values were: up to 15g, 16-19g, and 20g plus. Body weights are easy to measure in the field, but may not be a precise index of age of the rodents. However, at least for *A. sylvaticus* there is little increase in the accuracy of age estimates even if several additional characters such as weight of eye lenses and tooth wear are also taken into account (Gurnell and Knee, 1984). Since in the present study weights were used to allocate individuals to just three broad age classes, misallocations are likely to be few.

Another potential pitfall of using classes based on body weights is that at certain times of the year growth may cease and animals may even lose weight slightly as they get older, as happens in some bank vole populations during winter (Crawley, 1970). To avoid this problem a SAS program (AGECLASS) was written with E. Le Boulengé to allocate individuals to age classes irreversibly (Appendix 1). For example, if an individual progressed from juvenile to subadult, it would not be considered as a juvenile again even if its weight fell back to the juveniles' weight range.

Except for the separation of age classes, all the estimates of demographic parameters described in this Section were calculated by the program CMR (Le Boulengé, 1985, 1987).

4.2.3 - Home ranges and distances moved between captures - Home range areas were estimated using the Minimum Convex Polygon method (MCP, Jennrich and Turner, 1969). This is the method most widely used to estimate home range areas for mammals; therefore results are comparable with most of the existing literature (Harris *et al.*, 1990). MCP home range estimates were calculated using the McPAAL program (Stuwe and Blowowiak, 1985). Both home range areas and average distance moved between successive captures were calculated from the coordinates of each capture point on a map of the whole Corner Complex. Any capture location in a grid was assigned to the nearest pair of coordinates on the overall map, taking into account trap distances and actual inter-grid distances and angles as shown in Figure 4.1. This conversion was performed by a SAS program (FCOORD) written with E. Le Boulengé for this purpose (Appendix 2).

For each species and sex, home range areas were estimated using all captures of each individual ("total home ranges"). Separate estimates for each season were also calculated, re-running the program with only the captures of each individual in the period April-June (spring) or July-September (summer) or October-December (autumn) or February-March (winter). All home range estimates (total and seasonal) were obtained only from those individuals captured five or more times. This criterion follows Lidicker (1966) and Murúa *et al.* (1986), among others.

Seasonal variation in home range area was tested using the Kruskal-Wallis test, a non-parametric analogue of ANOVA. I opted for Kruskal-Wallis because of marked differences in the number of home range estimates available for each season. A similar number of data in each group is an assumption of ANOVA (Zar, 1984). I also sought correlations between average home range areas in each season and population sizes of the species concerned. For this analysis, population sizes in each season were defined as the average population size in the months composing each season, as defined in the previous paragraph.

The accuracy of home range area estimates is likely to be dependent on the number of captures (or radio-tracking fixes) of the individual (Harris *et al.*, 1990). If the estimated home range areas are plotted against number of captures per individual, the number of captures at which the curve levels off should correspond to the number needed to provide an accurate estimate of trap-revealed home range size. In the present study estimates of home range areas are intended primarily for comparisons between species, sexes and seasons. However, to provide an insight on how accurately the estimates reflect actual home range sizes, total home range areas were plotted against number of captures, separately for each species and sex, and the best fit third order polynomial was drawn to help to describe the trends. Third order polynomials were preferred because first and

second order polynomials tend to produce monotonic functions which lose much information, while higher order polynomials often are misleading because a sharp inflection in the curve can be easily caused by a single data point.

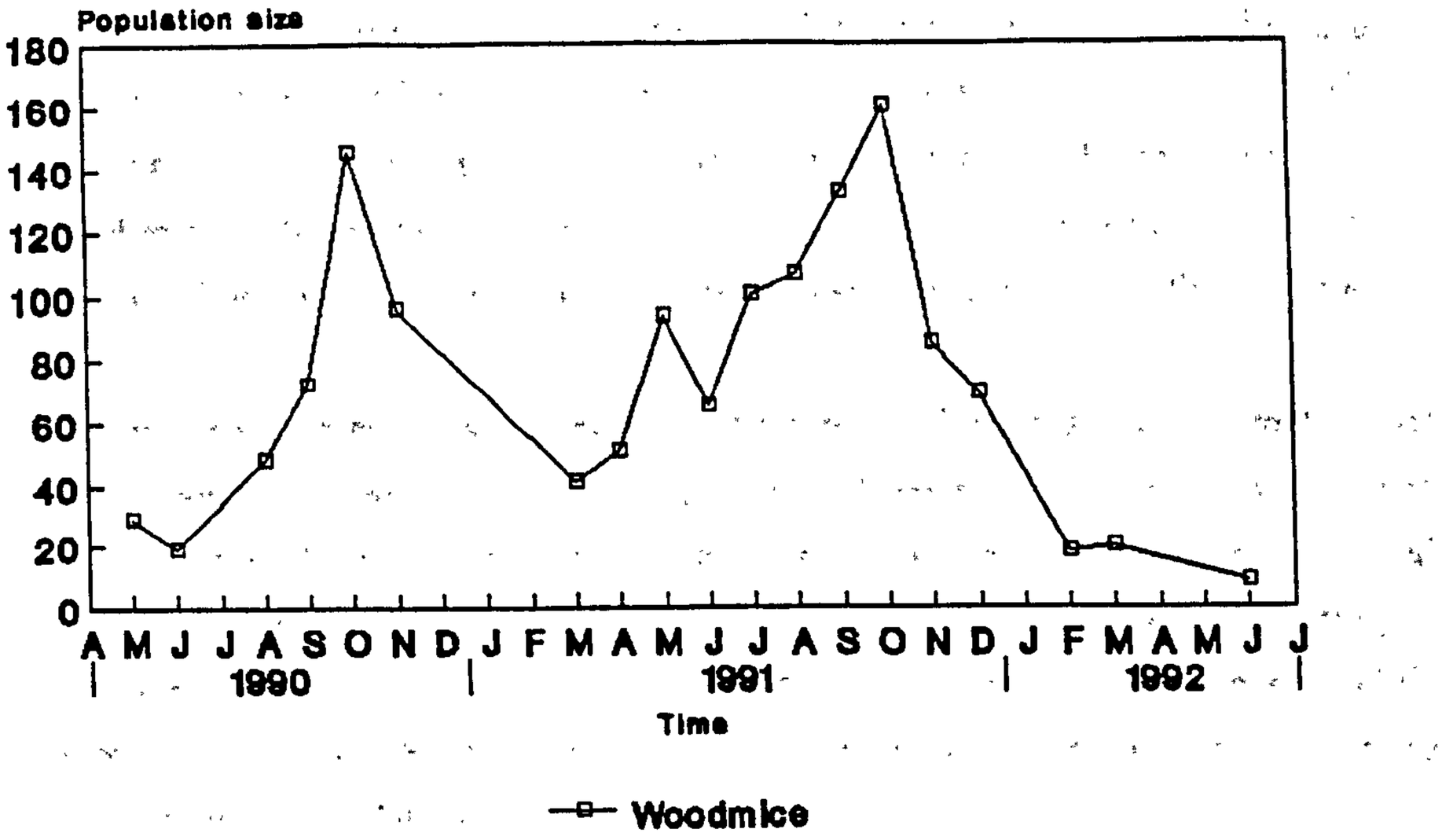
The average distance moved between successive captures was calculated using the program CMR, based on the overall coordinates calculated by FCOORD. This calculation was first performed for each species and sex using all captures of each individual. Estimates were also calculated separately by season, as with the home range estimates. Seasonal variation in average distance moved could not be tested statistically, because CMR outputs average distances moved by each individual, without giving the variance of these averages, i.e., the variance of the distance moved by each individual. Thus, the absences of variances and ranked orders by individual movements prevented the use of ANOVA and Kruskal-Wallis respectivelly. However, the correlation between average extension of movements in each season and the corresponding population size was calculated just as done for seasonal home ranges. This analysis involves the untested assumption that the distribution of individual movements did not differ significantly from normal within each season, i.e., that the averages were valid estimators of the central tendency of the distributions.

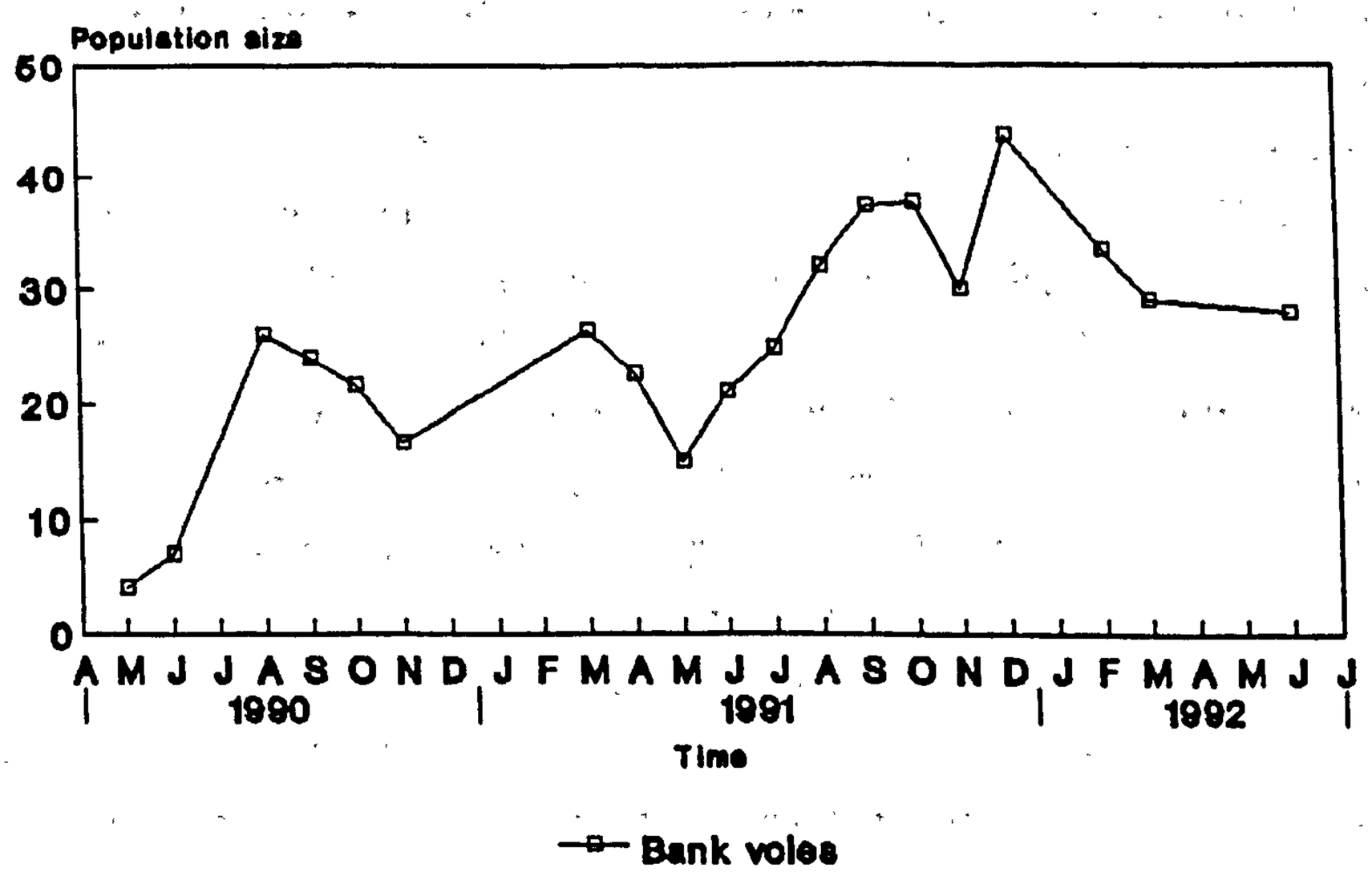
4.3 - Results

4.3.1 - Abundances of each rodent species; corrected versus uncorrected estimates - Population size estimates using (1) data corrected for number of grids and (2) uncorrected data were calculated for the two most abundant rodent species, woodmice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*). Results of the correlations between population size estimates and the other demographic parameters, home range areas and movements were compared across the two types of population estimates. In every single case, correlations were statistically significant or not, regardless of which set of population size estimates was used. All the results that follow are based on the original (uncorrected) estimates (the corresponding results based on the corrected estimates are shown in Appendix 3).

The monthly variations in population sizes of woodmice and bank voles are shown in Figure 4.2. Data for June 1992 are number of different individuals caught, because Manly-Parr estimates for this month could not be calculated because of the three-month gap from the previous trapping in all grids. Consequently, population size estimates for that month were not used when calculating correlations with any demographic parameters,

FIGURE 4.2. Monthly variation of population sizes of woodmice and bank voles in the Corner Complex, as estimated by the Manly-Parr method. Data from Tables 4.1 and 4.3.





but nevertheless they are shown in Figure 4.2 just to illustrate the population trends by the end of the study. From May 1990 to March 1992, population sizes of the two species were not significantly correlated to each other ($r = 0.346$, $p > 0.10$, 17 d.f.).

Field voles (*Microtus agrestis*) were not captured within the Corner Complex during most of the study. However, one to three individuals were captured in autumn 1990 and spring 1991 and, after the species had been absent for one year, a single individual was captured at the last trapping session in June 1992 (see Chapter 5). Calculation of demographic estimates was not feasible for this species due to its rarity in the study area, and therefore its demography is not discussed any further in this Chapter.

4.3.2 - Population dynamics of woodmice - Estimates of demographic parameters for *Apodemus sylvaticus* are presented in Table 4.1. In both years of the study, woodmice populations had a phase of low numbers in spring and early summer, followed by a marked increase by late summer and autumn, and remained high until December. However, in 1991 numbers were generally higher than in 1990 and the increase started earlier (July 1991, compared to August / September 1990). On the other hand numbers fell more sharply through the winter in 1991-92 than in 1990-91 (Figure 4.2).

Estimated daily trappabilities for woodmice were above 0.8 in most cases. The main exceptions were around and just after the time of felling in 1990 and in spring 1991 (Table 4.1).

Total survival (Table 4.1) was highest at the start of the population increase in both years, but fell sharply by the time peak numbers were reached in October-November (Figure 4.3). Although total survival was not significantly correlated with population size in the same month ($r = 0.252$, $p > 0.20$, $n = 16$), it was negatively correlated with population size in the previous month ($r = -0.591$, $p < 0.01$, $n = 15$). This "delayed" correlation was not significant for any age class taken separately, the highest correlation being between adult survival at t and population size at t - 1 ($r = -0.247$, $p > 0.20$, $n = 16$).

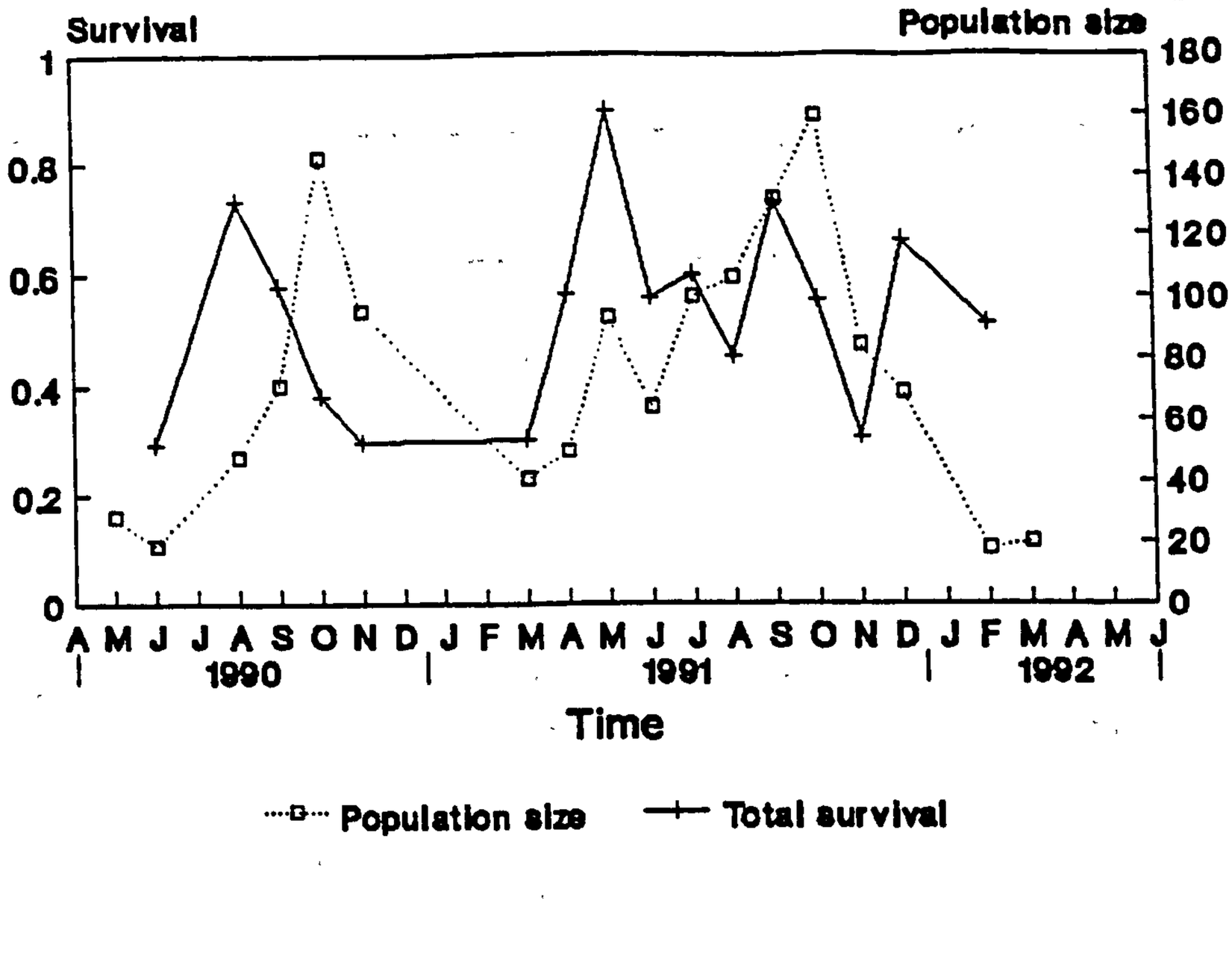
Examination of survival rates separated by age class showed contrasting patterns of variation for different age classes (Table 4.2). Patterns for subadult survival were erratic, sometimes similar to adult survival (e.g. June 1990, May 1991) and sometimes to juvenile survival (e.g. October 1990, December 1991). A clearer pattern emerged when juvenile and adult survival rates were compared. Overall, there was only a positive, non-significant correlation between adult and juvenile survival ($r = 0.183$, $p > 0.20$, $n = 16$), but there were interesting contrasts in the variation of the two rates along the study (Figure 4.3). Adult survival was higher than juvenile survival throughout 1990, except in September, during the population increase. In spring and summer 1991, survival of

TABLE 4.1. Estimates of demographic parameters for woodmice (*Apodemus sylvaticus*) in the Corner Complex, using the Manly-Parr method: population sizes, 30-day survival rates and daily trappabilities.

Time		Population size	Survival rate	Daily trapp.
1990	May	29.00 ± 0.00	-	1.000
	Jun	19.00 ± 0.00	0.293	1.000
	Jul	(18.00 ± 6.71)	(0.138)	(0.667)
	Aug	48.00 ± 18.97	0.735	0.667
	Sep	72.00 ± 18.59	0.580	0.625
	Oct	145.71 ± 34.06	0.381	0.583
	Nov	96.00 ± 5.66	0.296	0.938
	Dec	(78.00 ± 30.59)	(0.432)	(0.500)
1991	Feb	(21.00 ± 0.00)	(0.444)	(1.000)
	Mar	41.00 ± 0.00	0.301	1.000
	Apr	50.60 ± 14.78	0.563	0.455
	May	93.50 ± 35.03	0.895	0.364
	Jun	64.80 ± 5.80	0.554	0.833
	Jul	100.36 ± 5.39	0.596	0.917
	Aug	106.11 ± 4.13	0.541	0.905
	Sep	132.00 ± 9.38	0.732	0.818
	Oct	159.71 ± 13.98	0.550	0.808
	Nov	84.58 ± 5.81	0.303	0.828
	Dec	68.83 ± 10.07	0.655	0.857
1992	Feb	18.29 ± 1.83	0.510	0.875
	Mar	20.00 ± 0.00	-	-
	Jun	(9)	-	-

Note. Estimates in parentheses are not comparable to the others because they are based on two or three grids only or, in the case of June 1992, because the population estimate for the last month is simply the number of different individuals caught (see text, Section 4.2.2). Traces (-) indicate cases where calculations were not feasible with the data available.

FIGURE 4.3. Monthly variation of woodmice survival rates. Top: overall survival, estimated by the Manly-Parr method, and its relationship with the variation of population sizes. Bottom: comparison of adult and juvenile survival, both estimated by P_{min}. Data from Tables 4.1 and 4.2.



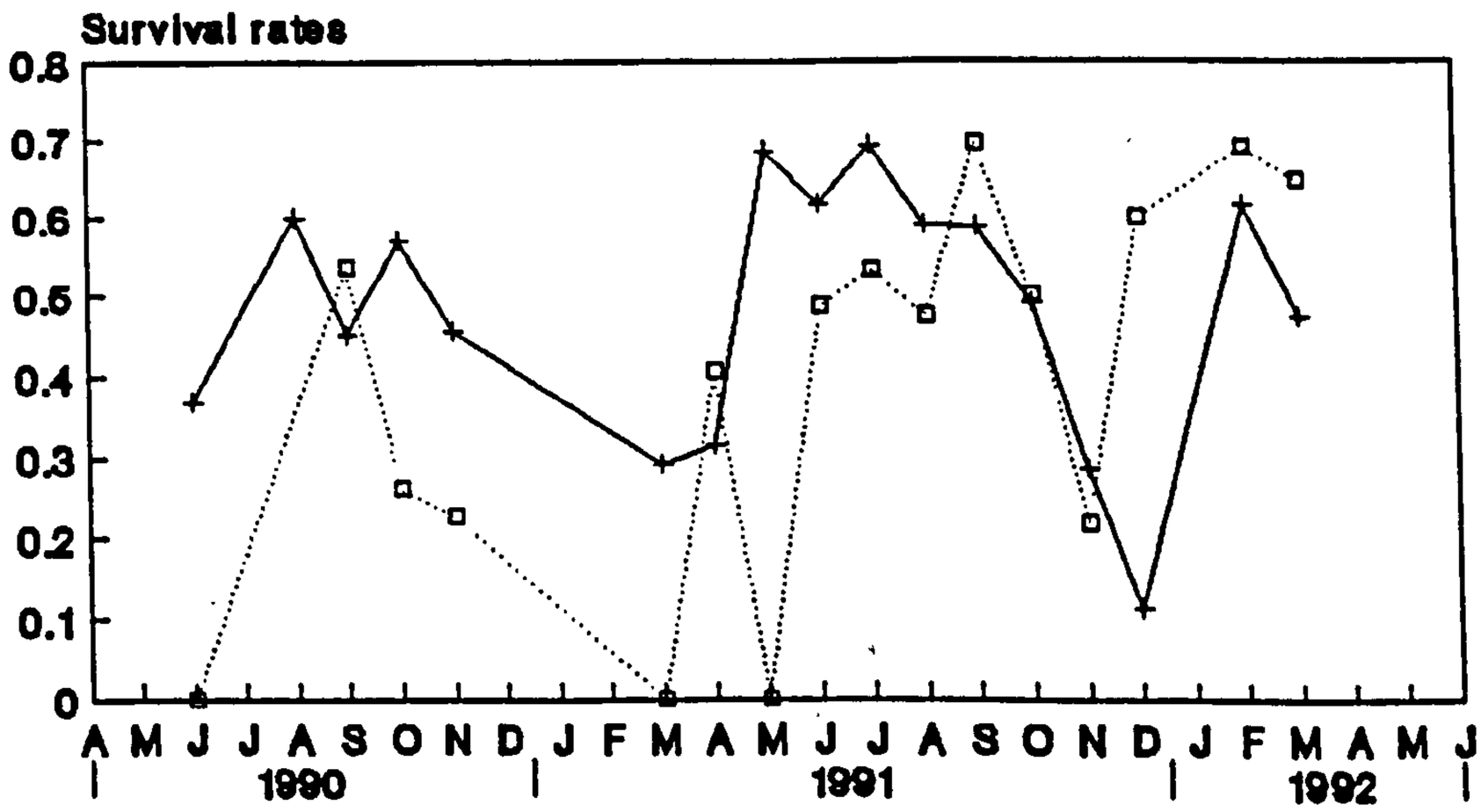


TABLE 4.2. Estimates of demographic parameters for *Apodemus sylvaticus* in the Corner Complex: 30-day minimum survival rates (P_{min}) for each age class, 30-day juvenile recruiment rates and proportion of reproductive subadult or adult females.

Time	Survival juveniles	Survival subadults	Survival adults	Recruitment juveniles	Proportion reproductive females (n)
1990					
May	-	-	-	-	0.778 (9)
Jun	0.000	0.380	0.369	0.073	1.000 (9)
Jul	(0.000)	(0.000)	(0.226)	(0.000)	(0.750 (4))
Aug	-	0.375	0.599	0.112	0.857 (14)
Sep	0.535	0.690	0.450	0.180	1.000 (10)
Oct	0.260	0.150	0.570	0.220	0.917 (12)
Nov	0.226	0.520	0.455	0.331	0.364 (22)
Dec	(0.232)	(0.232)	(0.146)	(0.147)	(0.000 (9))
1991					
Feb	(0.406)	(0.000)	(0.610)	(0.017)	(0.333 (3))
Mar	0.000	0.540	0.289	0.105	0.667 (12)
Apr	0.405	0.491	0.313	0.052	0.800 (5)
May	0.000	0.648	0.688	0.053	1.000 (11)
Jun	0.488	0.488	0.620	0.255	0.765 (17)
Jul	0.533	0.533	0.695	0.299	0.958 (24)
Aug	0.476	0.591	0.591	0.321	0.897 (29)
Sep	0.698	0.743	0.589	0.240	0.708 (24)
Oct	0.502	0.491	0.491	0.260	0.061 (33)
Nov	0.217	0.375	0.285	0.089	0.000 (21)
Dec	0.603	0.627	0.111	0.040	0.000 (21)
1992					
Feb	0.693	0.463	0.618	0.024	0.167 (6)
Mar	0.651	0.537	0.476	0.107	0.625 (8)
Jun	-	-	-	0.000	1.000 (5)

Note. Number of adult and subadult females captured at each month is given in parentheses in the last column. Remaining symbols as in Table 4.1.

juveniles was again the poorer in all months except April. In autumn 1991 the two groups had similar survival rates, and in contrast to the previous year, juveniles survived better than adults through the winter 1991-92.

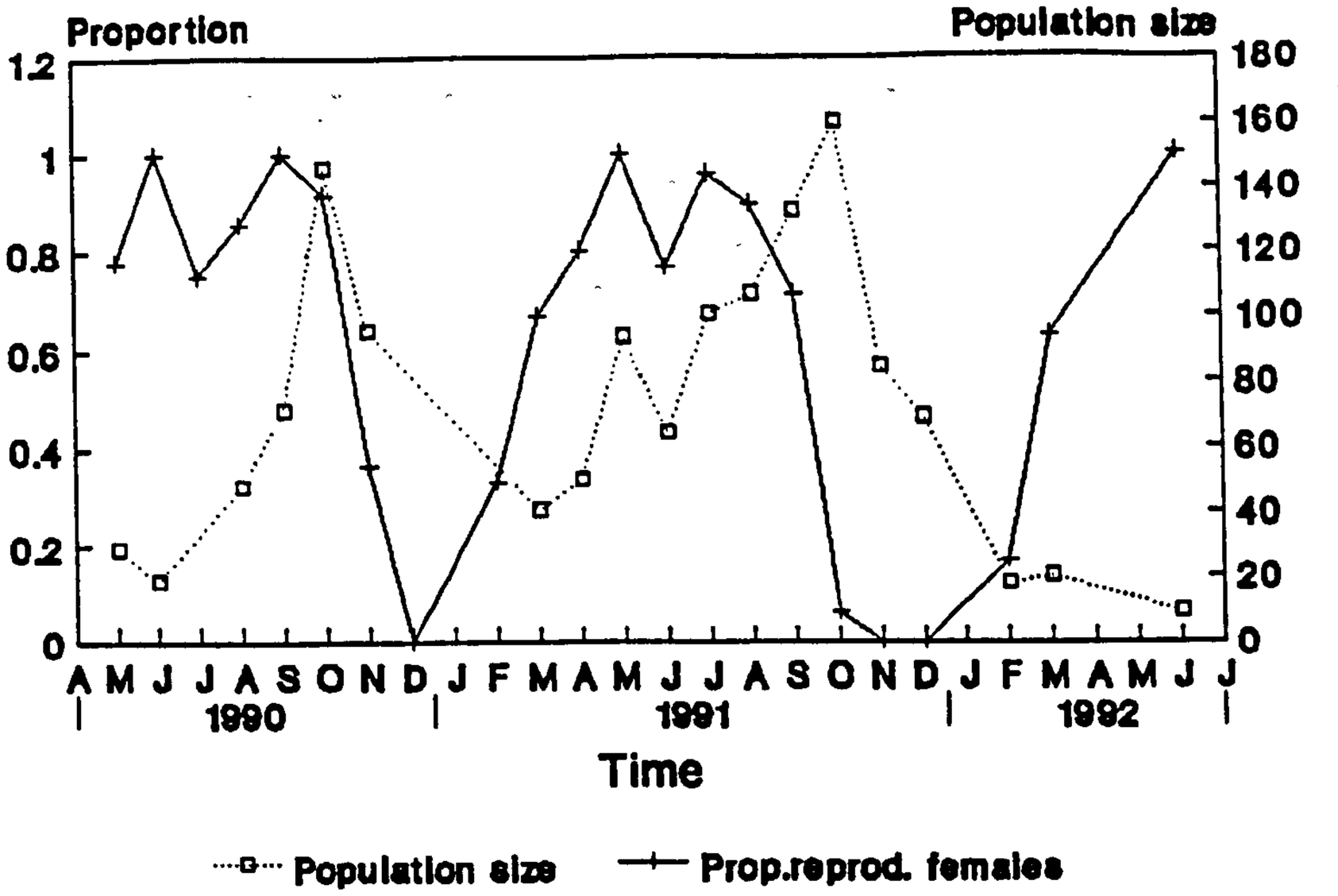
The proportion of reproductive female woodmice (Table 4.2) was high during most of each year of study, but it fell in both autumns, reached zero in both Decembers and recovered gradually during the springs of 1991 and 1992 (Figure 4.4). The only marked difference between the years was that proportion of reproductive females fell earlier in 1991 than in 1990: by October 1990 more than 90% of the subadult or adult females in the population were still in reproductive condition, while in October of the following year the proportion was only 6.1%. The proportion of reproductive females was not correlated with population size in the same month ($r = -0.063$, $p > 0.50$, $n = 17$), but it showed a significant negative correlation with population size in the previous month ($r = -0.583$, $p < 0.01$, $n = 16$; Figure 4.4). Among all the remaining demographic parameters measured for woodmice, the proportion of reproductive females showed a positive correlation only with adult survival ($r = 0.478$, $p < 0.05$, $n = 17$).

Variation in juvenile recruitment rates was closely coupled with variation in population size (Figure 4.4), resulting in a significant positive correlation ($r = 0.640$, $p < 0.01$, $n = 17$). An interesting finding was that juvenile recruitment was zero by the end of the study in June 1992, in spite of the proportion of reproductive females at that month being 1.000 (five out of five). Juvenile recruitment also showed a significant negative correlation with adult survival ($r = -0.475$, $p < 0.05$, $n = 17$). All other correlations among demographic parameters for woodmice were non-significant.

4.3.3 - Population dynamics of bank voles - The variation in numbers of *Clethrionomys glareolus* was very different from that of *A. sylvaticus*. In 1990, bank voles were consistently less abundant than woodmice, and the population peak was reached in summer (August) rather than autumn (Table 4.3, Figure 4.2). Bank vole populations remained relatively high in the winter of 1990-91, and fell only slightly in spring 1991. After that the increase in numbers started earlier (June) than the increase in woodmice and high numbers were sustained through the autumn leading to a December peak. In contrast to woodmice, bank voles were still abundant by the end of the study in June 1992 (Figure 4.2).

Estimated daily trappabilities were lower for bank voles than for woodmice, although the lowest values were found at a similar time for the two species: autumn 1990, just after felling, and spring 1991 (Table 4.3).

FIGURE 4.4. Monthly variation of woodmice reproduction and recruitment, and its relationship with the variation in population sizes. Top: proportion of reproductive females; bottom: juvenile recruitment. Data from Tables 4.1 and 4.2.



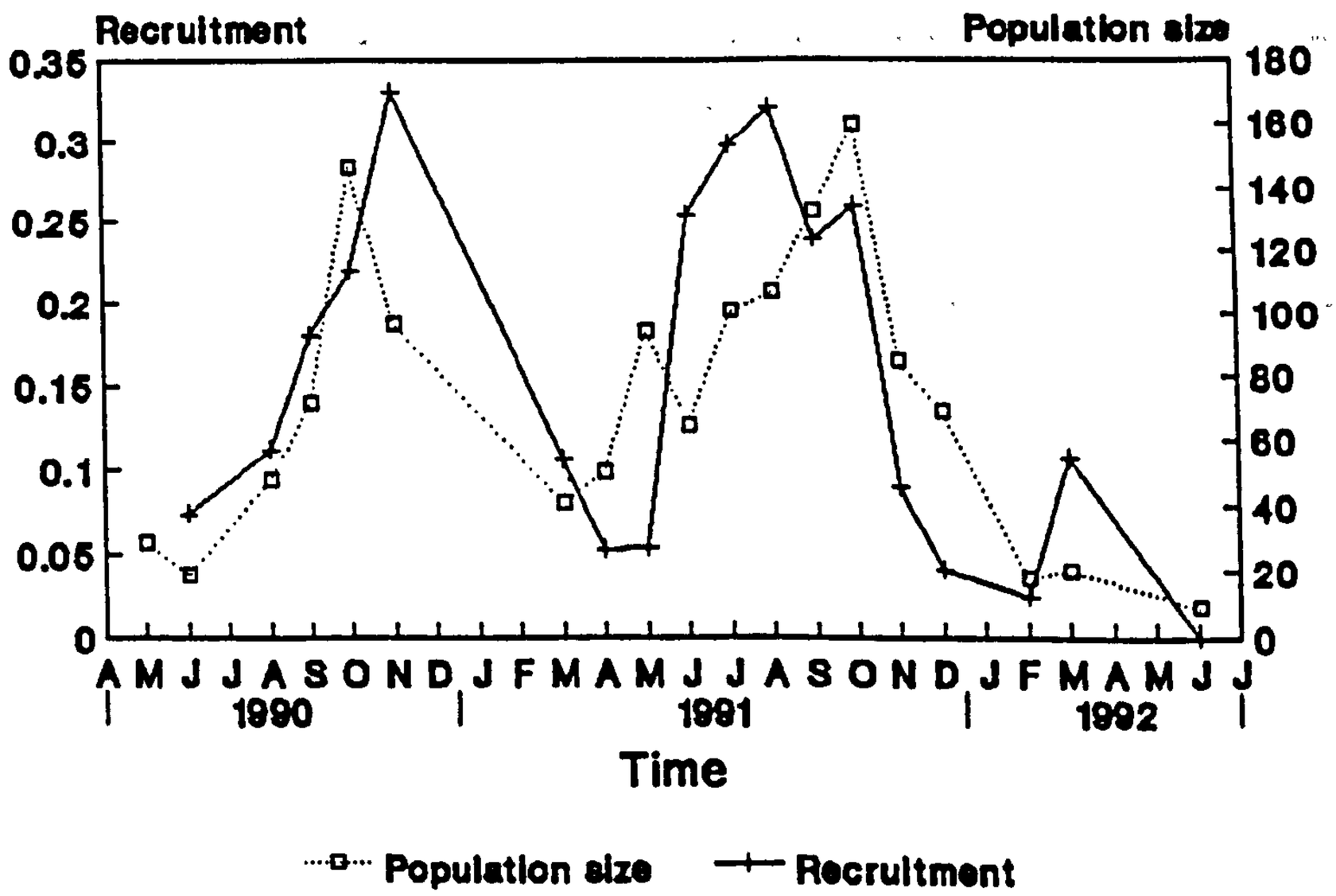


TABLE 4.3. Estimates of demographic parameters for bank voles (*Clethrionomys glareolus*) in the Corner Complex, using the Manly-Parr method: population sizes, 30-day survival and daily trappability. Symbols as in Table 4.1.

Time		Population size	Survival	Daily trapp.
1990	May	4.00 ± 0.00	-	-
	Jun	7.00 ± 0.00	-	-
	Jul	(18.00 ± 12.00)	-	(0.500)
	Aug	26.00 ± 0.00	0.308	1.000
	Sep	24.00 ± 8.94	0.485	0.333
	Oct	21.60 ± 3.35	0.600	0.833
	Nov	16.67 ± 5.09	0.355	0.600
	Dec	(8.00 ± 0.00)		
1991	Feb	(20.00 ± 9.49)	-	(0.400)
	Mar	26.25 ± 7.36	1.000	0.571
	Apr	22.50 ± 10.87	1.000	0.400
	May	15.00 ± 0.00	0.503	1.000
	Jun	21.00 ± 3.74	0.691	0.667
	Jul	24.75 ± 3.41	0.803	0.727
	Aug	32.00 ± 5.66	0.490	0.750
	Sep	37.50 ± 7.02	0.532	0.533
	Oct	37.71 ± 7.60	0.555	0.583
	Nov	30.00 ± 3.87	0.522	0.667
	Dec	43.75 ± 8.35	1.000	0.571
1992	Feb	33.60 ± 4.34	0.810	0.714
	Mar	29.00 ± 0.00	-	-
	Jun	(28)	-	-

Overall survival of bank voles was in most cases higher in 1991 than in the corresponding months of the previous year (Table 4.3). No significant correlation could be found between total survival and population size, with or without a time lag ($r = 0.168$, $n = 15$ and $r = 0.268$, $n = 14$ respectively; either, $p > 0.20$; Figure 4.5).

Adult survival (Table 4.4) was significantly correlated with population size in the same month ($r = 0.635$, $p < 0.01$, $n = 17$) and the previous month as well ($r = 0.478$, $p < 0.05$, $n = 16$). Adult survival was very good through the winter of 1991-92, when high numbers were sustained (Figure 4.5). The correlation between population size and juvenile survival was marginally non-significant ($r = 0.368$, $0.05 < p < 0.10$, $n = 16$), and no correlation at all was found between population size and subadult survival ($r = -0.020$, $p > 0.50$, $n = 17$).

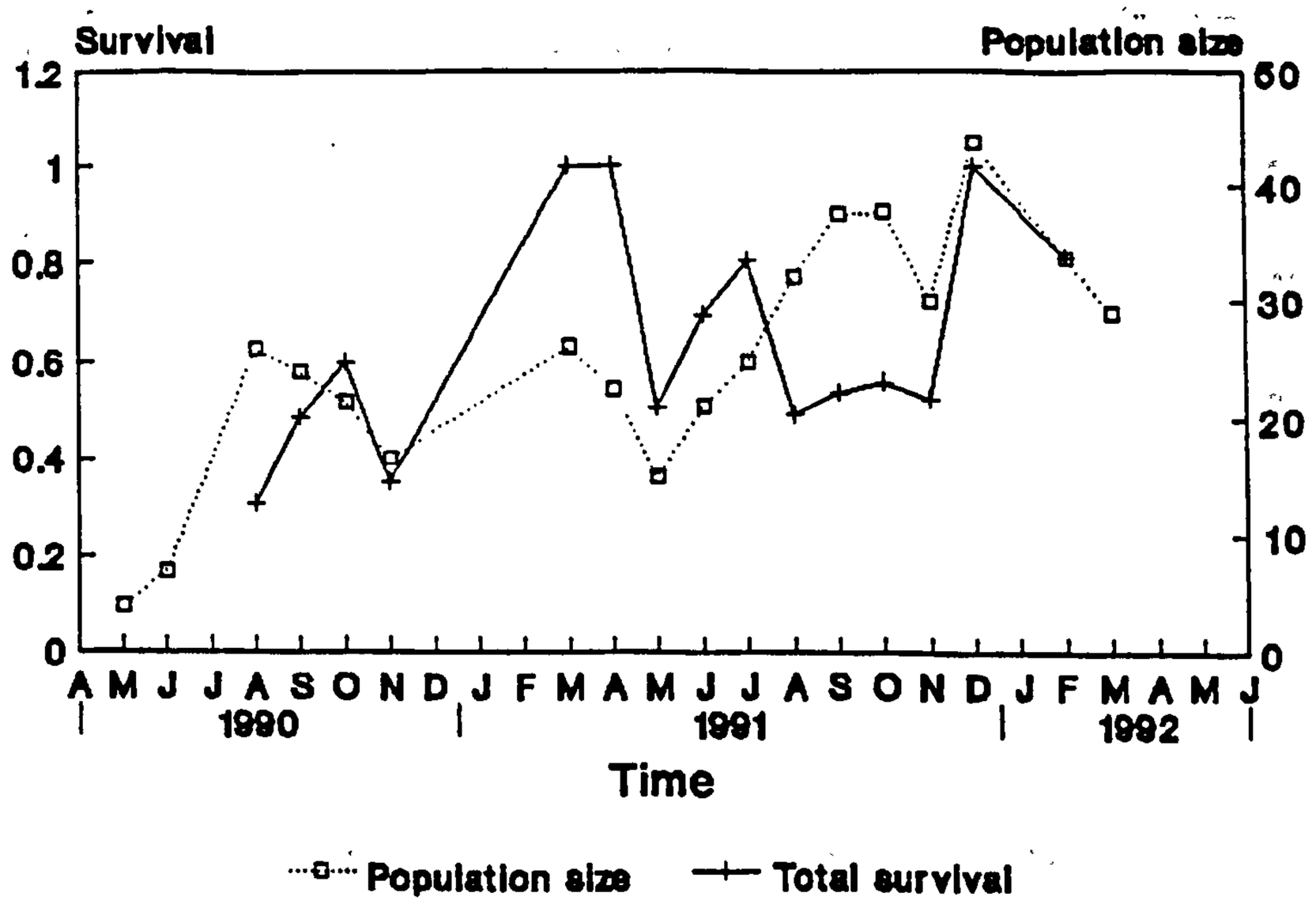
Survival of adult and juvenile bank voles followed very similar patterns in the first year of study, but very different in the second (Table 4.4, Figure 4.5). Survival of both age classes increased through summer and early autumn 1990, fell sharply in November, but recovered by spring 1991; in this period survival of the two age groups was positively correlated ($r = 0.826$, $p < 0.05$, $n = 6$). From then on adult survival was higher than juvenile survival in every single month except September 1991 and February 1992, the gap between the two rates being greatest in autumn 1991. However, survival was very good in both groups over the winter 1991-92, when high numbers were sustained. The negative correlation between the survival of the two age groups in the second year was non-significant ($r = -0.404$, $p > 0.10$, $n = 8$).

Reproductive female bank voles were captured in every month except December 1990 and February 1992 (Table 4.4). As in woodmice, there was evidence of a short interruption of breeding in winter, followed by a quick recovery to a high proportion of reproductive females by March in both years. A comparison between the two years of the study shows some marked differences. The proportion of reproductive females in 1991 was always higher than in the corresponding months of 1990 until August (Figure 4.6). Thereafter, during the early stages of the period of high numbers (autumn 1991), a much smaller proportion of females was reproductive than during the corresponding months in 1990. On the other hand, breeding apparently stopped at least one month later in 1991 than in 1990. The proportion of reproductive females in bank voles was negatively correlated with population size at the same month ($r = -0.419$, $p < 0.05$, $n = 17$) and with population size in the previous month as well ($r = -0.707$, $p < 0.01$, $n = 16$; Figure 4.6), but positively correlated with adult survival in the previous month ($r = 0.479$, $p < 0.05$, $n = 16$).

TABLE 4.4. Estimates of demographic parameters for *Clethrionomys glareolus* in the Corner Complex: monthly variations of 30-day minimum survival rates (P_{min}) for each age class, 30-day juvenile recruiment rates and proportion of reproductive subadult or adult females. Symbols as in Table 4.2.

Time	Survival juveniles	Survival subadults	Survival adults	Recruitment juveniles	Proportion reproductive females
1990					
May	-	-	-	-	0.500 (4)
Jun	-	1.000	0.000	0.100	0.429 (7)
Jul	(0.000)	(0.476)	(0.000)	(0.119)	(1.000 (4))
Aug	0.000	1.000	0.305	0.165	0.667 (18)
Sep	0.623	0.470	0.410	0.088	0.500 (14)
Oct	0.500	1.000	0.710	0.231	0.500 (6)
Nov	0.141	0.058	0.430	0.106	0.800 (5)
Dec	(0.205)	(0.371)	(0.371)	(0.179)	(0.000 (1))
1991					
Feb	(0.000)	(1.000)	(0.902)	(0.018)	(0.333 (3))
Mar	1.000	0.226	1.000	0.025	0.714 (7)
Apr	0.593	0.000	0.834	0.000	1.000 (4)
May	-	0.648	0.648	0.000	0.875 (8)
Jun	-	0.743	0.630	0.197	1.000 (8)
Jul	0.533	1.000	0.835	0.147	1.000 (10)
Aug	0.287	0.389	0.688	0.469	1.000 (9)
Sep	0.933	0.315	0.617	0.133	0.400 (5)
Oct	0.449	0.555	1.000	0.214	0.286 (7)
Nov	0.246	0.893	1.000	0.214	0.125 (8)
Dec	0.713	0.879	1.000	0.249	0.333 (9)
1992					
Feb	0.908	0.801	0.671	0.078	0.000 (6)
Mar	0.693	0.735	1.000	0.148	0.667 (6)
Jun	-	-	-	0.071	0.750 (8)

FIGURE 4.5. Monthly variation of bank vole survival rates. Top: overall survival, estimated by the Manly-Parr method, and its relationship with the variation of population sizes. Bottom: comparison of adult and juvenile survival, both estimated by P_{min}. Data from Tables 4.3 and 4.4.



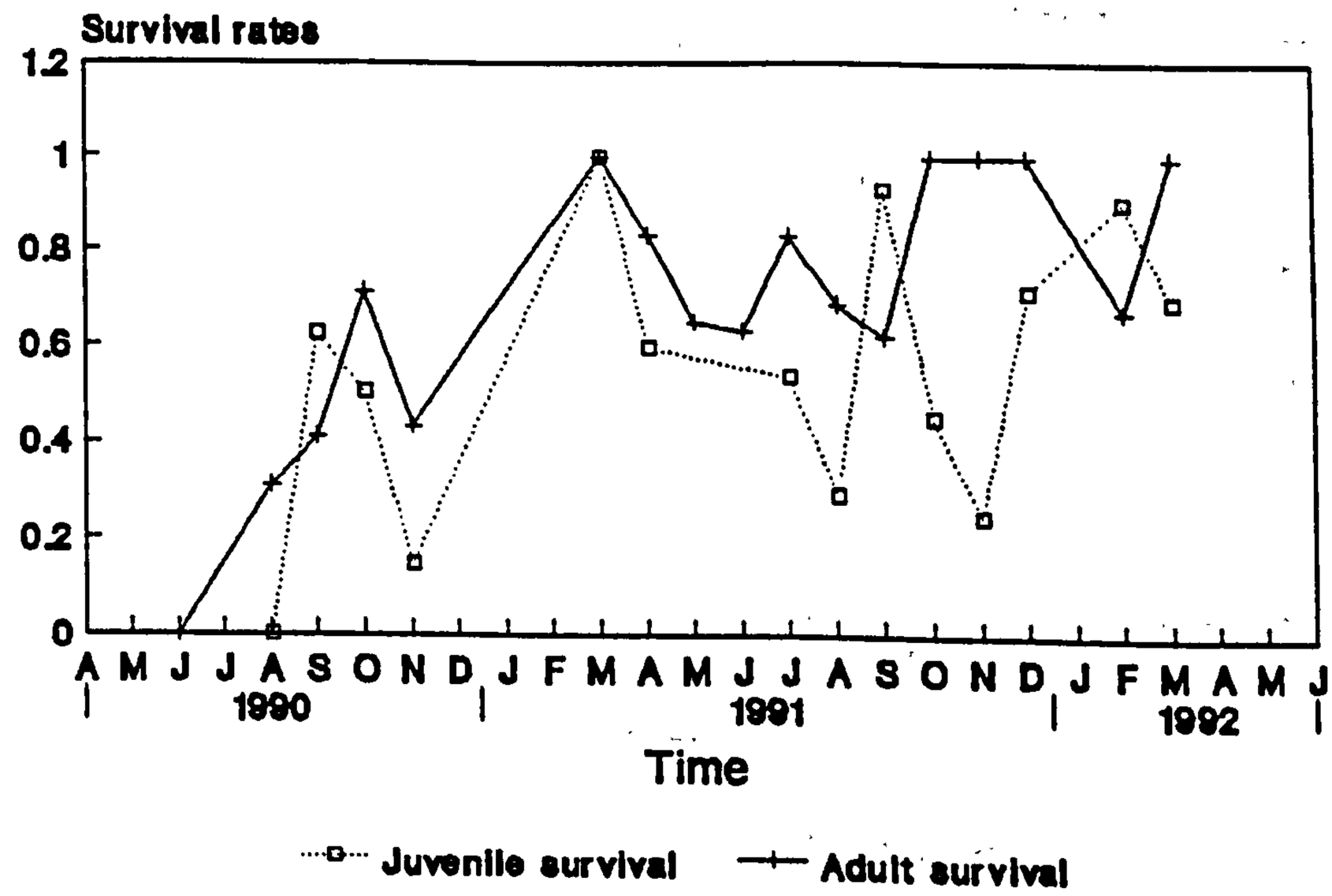
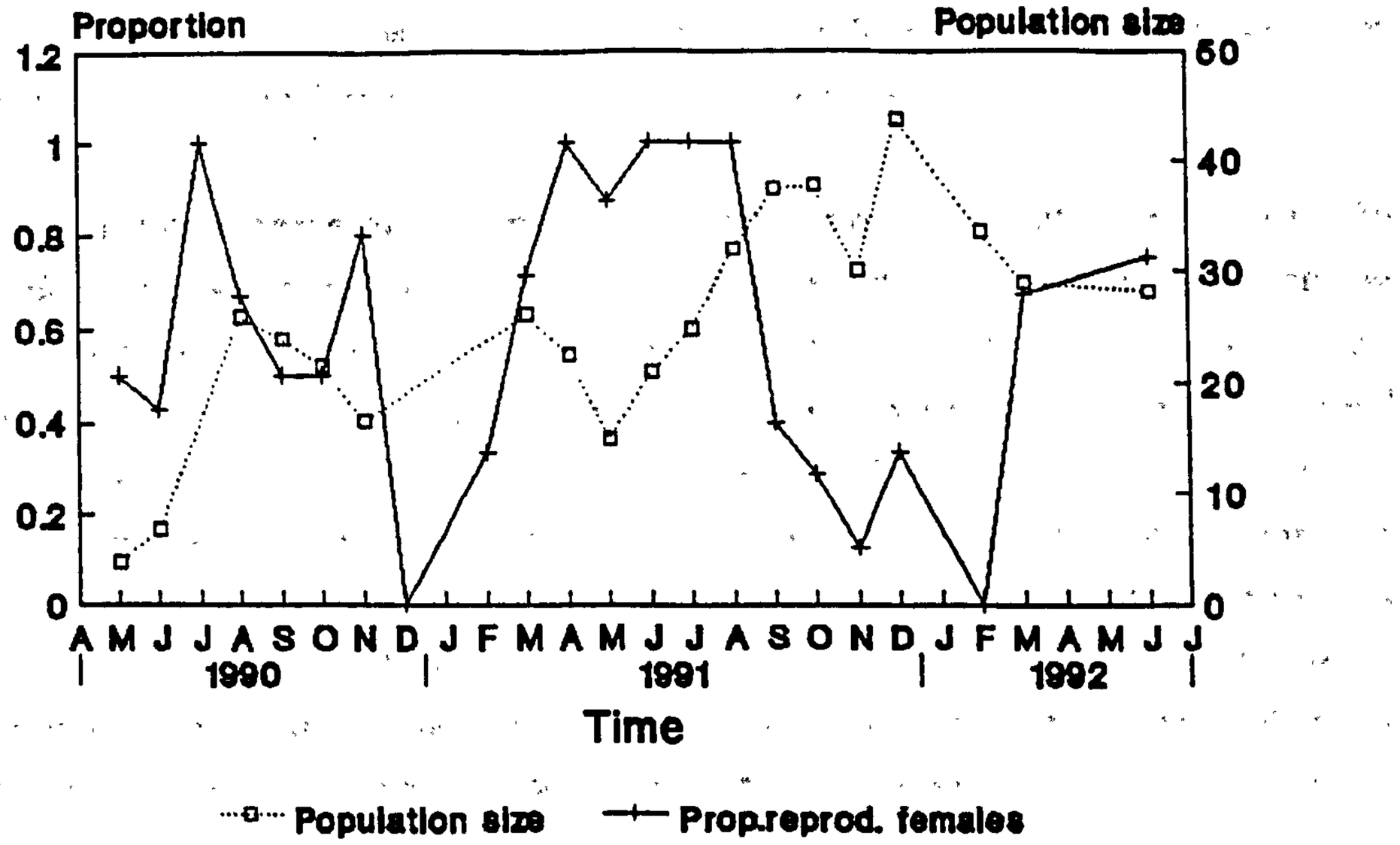
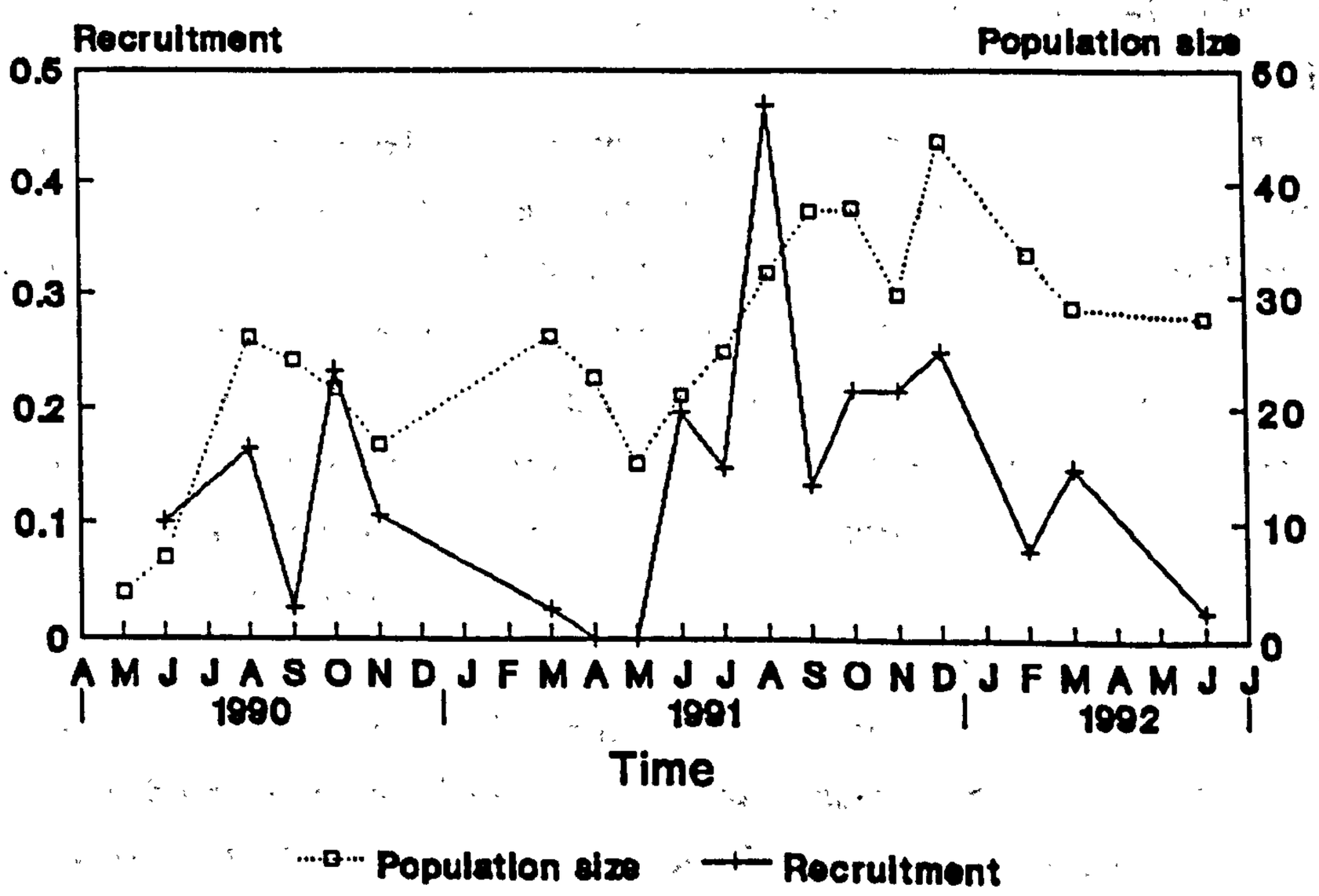


FIGURE 4.6. Monthly variation of bank vole reproduction and recruitment, and its relationship with the variation in population sizes. Top: proportion of reproductive females; bottom: juvenile recruitment. Data from Tables 4.3 and 4.4.





As in woodmice, bank vole population sizes until March 1992 were positively correlated with juvenile recruitment rates ($r = 0.421$, $p < 0.05$, $n = 17$; Figure 4.6). However, juvenile recruitment was low in June 1992, by the time of the sustained high numbers in the end of the study (Figure 4.6). Juvenile recruitment rates were not significantly correlated with the survival rates of any age class.

4.3.4 - Home range areas and average distances moved - A high proportion of the home ranges from which areas could be calculated extended over more than one trapping grid. In woodmice, 70 out of 105 male home ranges (66.7%) and 33 out of 61 female home ranges (54.1%) included two or more grids. In bank voles, the proportions were 7 out of 16 for males (43.8%) and 3 out of 17 for females (17.6%). In most of such cases, the grids being used by a single individual belonged to different habitat types. The mature forest grid Corner North and the clear-felling Corner 2 were the pair most often used by individuals captured in more than one grid (see analysis of movements by grids in Chapter 6). As a whole, the results show that individuals (especially woodmice) were often not restricted to a single grid within the Corner Complex, thus supporting the assumption that the population of the area can be treated as a whole.

Estimates of total home range areas for individuals of each species and sex are presented in Tables 4.5 and 4.6 and plotted against number of captures in Figure 4.7. Home range area estimates levelled at about 10 captures for male bank voles and at about 20 captures for male woodmice. For female woodmice estimates seemed to level at about 10 captures. The apparent exponential increase at the right of the graph (Fig. 4.7b) is due not to the individual captured most often having a large home range, but rather to the individual with the second highest number of captures having a small home range, thus causing the upward bend of the polynomial function. For female bank voles there was little evidence of the curve levelling at all. Thus the values I obtained for both species and both sexes, which were based on all individuals caught five or more times, probably underestimated true home range sizes to some extent. Nevertheless those values are useful for comparisons between seasons and sexes, and indeed several patterns emerge from these comparisons, as follows.

Male woodmice had significantly larger total home range areas than female woodmice ($t = 2.461$, $p < 0.01$). This pattern was found in all seasons, but the difference was small in both autumns (Table 4.5). Female home ranges showed little seasonal variation (Kruskal-Wallis, $H = 2.053$, $p > 0.90$), but male home ranges varied significantly with season (Kruskal-Wallis, $H = 15.461$, $p < 0.05$). Male home range areas were larger at the time of lowest densities, i.e., spring and summer 1990, winter 1990-91 and spring

TABLE 4.5. Home ranges and movements of woodmice in the Corner Complex. Top: home range areas as estimated by the Minimum Convex Polygon method. Bottom: average distances moved between successive captures.

Home ranges sizes (ha)	Males	Females
Overall	0.407 ± 0.379 (105)	0.294 ± 0.358 (61)
1990		
Winter	0.029 (1)	-
Spring	0.862 ± 1.078 (2)	0.161 ± 0.194 (2)
Summer	0.550 ± 0.465 (3)	0.198 ± 0.082 (3)
Autumn	0.242 ± 0.217(19)	0.214 ± 0.217 (8)
1991		
Winter	0.533 ± 0.380 (7)	0.158 ± 0.056 (4)
Spring	0.621 ± 0.292 (6)	0.241 ± 0.272 (6)
Summer	0.283 ± 0.272 (30)	0.177 ± 0.177 (16)
Autumn	0.277 ± 0.188 (28)	0.201 ± 0.191 (15)
1992		
Winter	0.378 ± 0.338 (3)	0.239 ± 0.172 (3)

Average distances moved (m)	Males	Females
Overall	48.4 (1124)	39.9 (646)
1990		
Winter	34.5 (22)	27.4 (15)
Spring	48.8 (38)	24.5 (38)
Summer	57.1 (49)	26.7 (33)
Autumn	39.4 (162)	42.6 (91)
1991		
Winter	58.2 (73)	38.4 (27)
Spring	71.2 (65)	40.0 (47)
Summer	41.3 (271)	42.4 (156)
Autumn	43.6 (306)	34.2 (151)
1992		
Winter	57.0 (37)	47.4 (30)

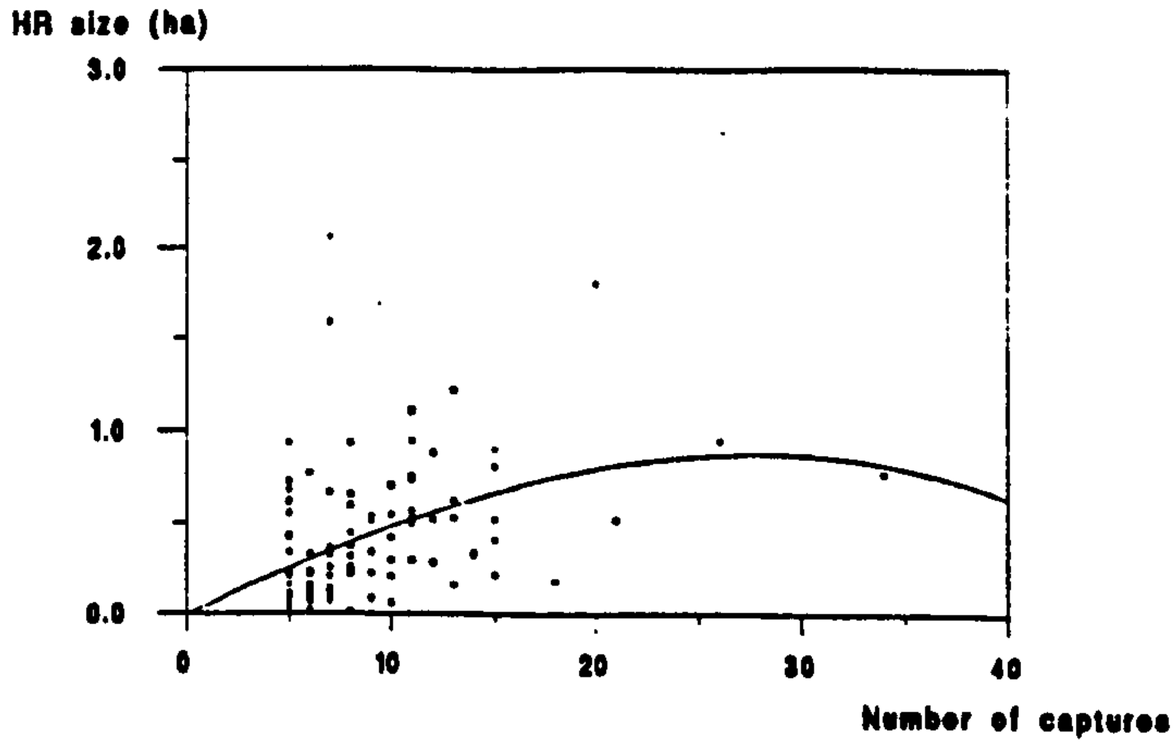
Note. Values presented for home range areas are means ± s.d; sample sizes (number of individuals) in parentheses; for movements, values are the averages, with sample sizes (number of movements) in parentheses.

TABLE 4.6. Home ranges and movements of bank voles in the Corner Complex. Top: home range areas as estimated by the Minimum Convex Polygon method. Bottom: average distances moved between successive captures.

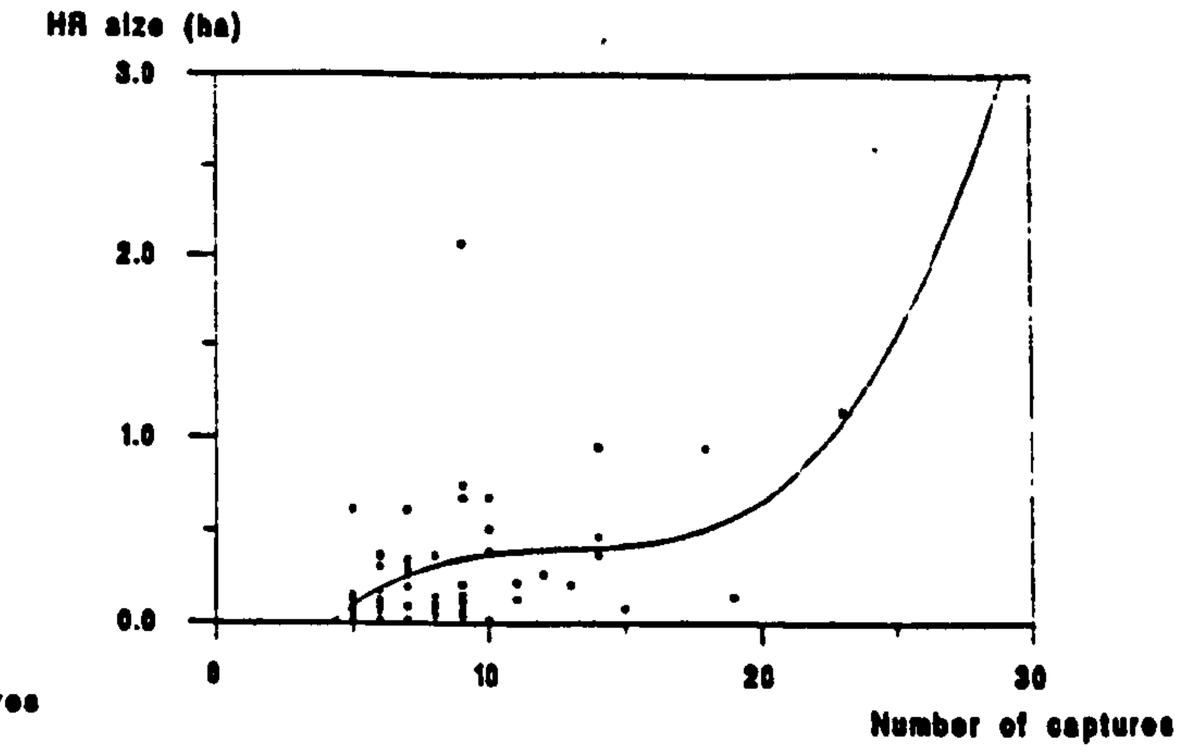
Home range sizes (ha)	Males	Females
Overall	0.191 ± 0.187 (16)	0.136 ± 0.156 (17)
1990		
Winter	-	-
Spring	-	-
Summer	0.075 ± 0.093(3)	0.085 ± 0.035 (3)
Autumn	0.059 (1)	0.038 (1)
1991		
Winter	0.189 ± 0.174 (2)	-
Spring	0.055 (1)	0.066 (1)
Summer	-	0.041 ± 0.023 (2)
Autumn	-	0.143 ± 0.035 (3)
1992		
Winter	0.039 ± 0.017 (2)	0.036 ± 0.009 (2)

Average distance moved (m)	Males	Females
Overall	33.2 (150)	22.5 (231)
1990		
Winter	-	30.3 (4)
Spring	-	20.6 (14)
Summer	32.7 (23)	22.8 (35)
Autumn	27.0 (9)	20.4 (17)
1991		
Winter	32.3 (14)	27.5 (10)
Spring	57.8 (13)	19.9 (23)
Summer	26.6 (12)	17.0 (27)
Autumn	16.6 (16)	28.2 (36)
1992		
Winter	18.2 (28)	24.5 (26)

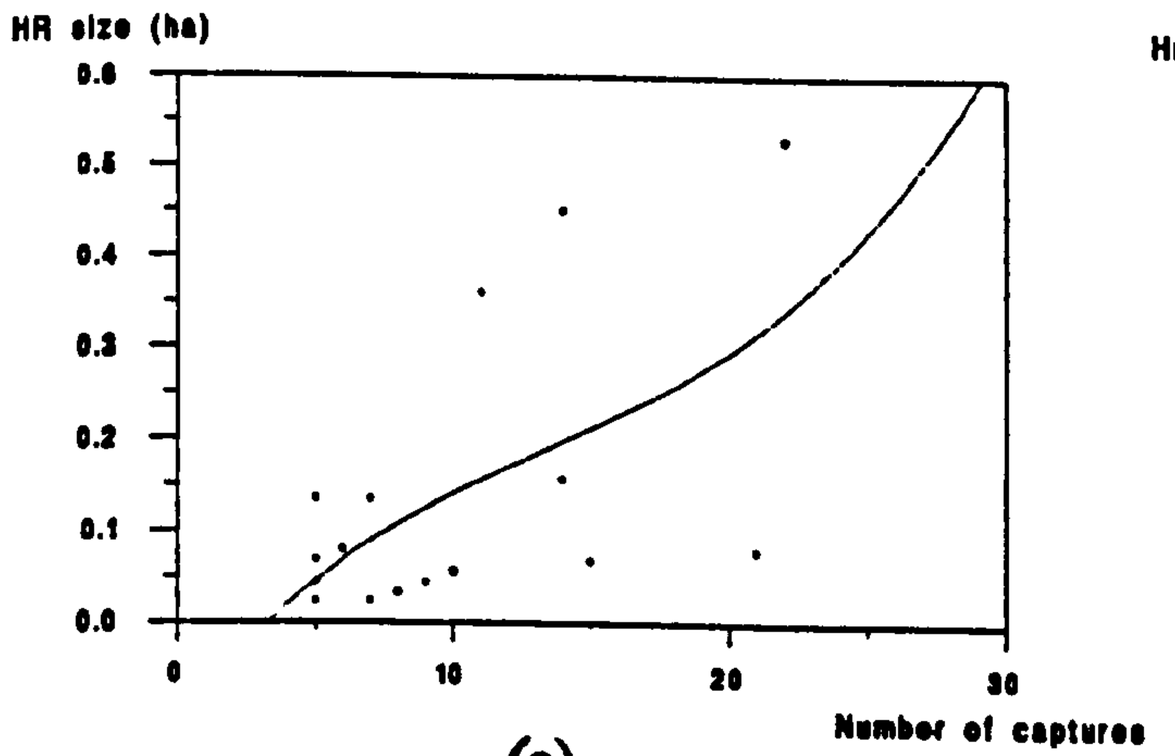
FIGURE 4.7. Relationship between number of captures per individual and the corresponding home range area estimates (in hectares). a) Male woodmice. b) Female woodmice. c) Male bank voles. d) Female bank voles. Curves are the third order polynomials which fit best the data.



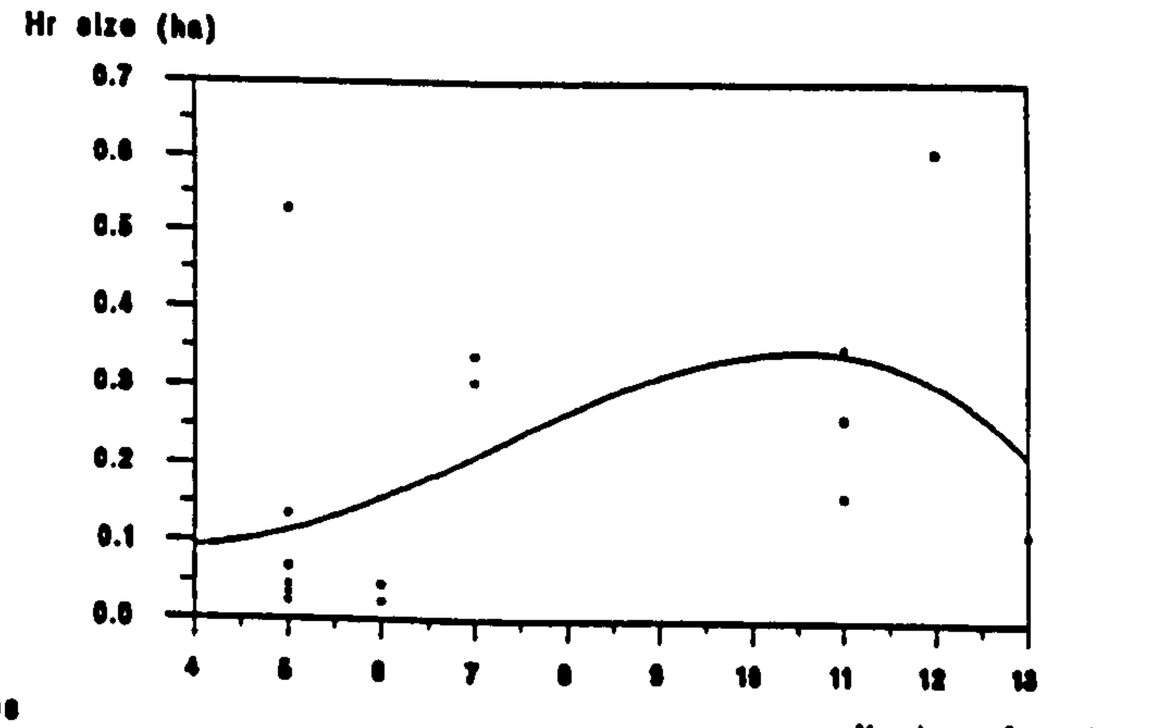
(a)



(b)

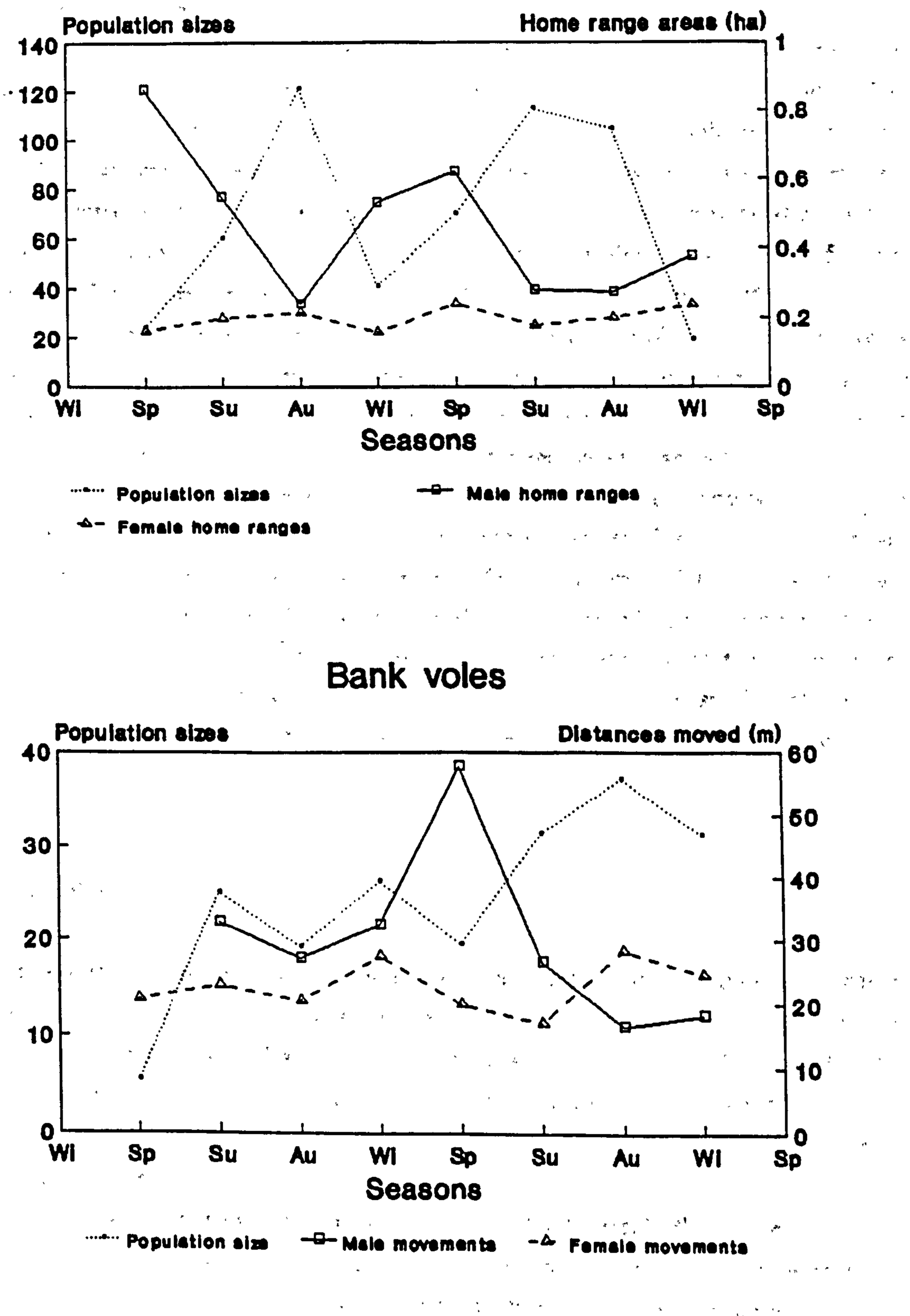


(c)



(d)

FIGURE 4.8. Seasonal variation of population sizes and its relationship with average home range areas of woodmice (top) and average distances moved by bank voles (bottom). Population sizes are given by the average population size during the season (Section 4.2.3).



1991 (Table 4.5). Indeed, male home range area showed a strong negative correlation with average population size at each season ($r = -0.706$, $p < 0.05$, $n = 8$ seasons; Figure 4.8). No significant correlation was found, however, between female home range area and seasonal population size ($r = 0.087$, $p > 0.50$, $n = 8$; Figure 4.8).

Patterns shown by the average distances moved by woodmice between captures were consistent with the variation in home range areas (Table 4.5). Males moved further than females only at times of low population size. At times of high population size (autumn 1990, summer and autumn 1991) the distances moved by males and females were similar. The correlation between average distance moved and average population size at each season was negative but marginally non-significant for males ($r = -0.573$, $0.05 < p < 0.10$); no significant correlation was obtained for females ($r = 0.235$, $p > 0.25$).

A smaller number of estimates of home range area were obtained for bank voles than for woodmice, thus seasonal patterns of variation in this parameter could not be tested statistically. Although there was a trend for male bank voles to have bigger home ranges than females (Table 4.6), the difference between sexes was not significant ($t = 0.837$, $p > 0.20$). However, patterns regarding distances moved between successive captures are clearer. Overall, males again moved further than females. This difference was apparent throughout a whole year from summer 1990 to summer 1991. The pattern was apparently reversed in autumn 1991 and winter 1992, the time of highest numbers of bank voles, when females moved further than males. As a consequence of these contrasting patterns for males and females, average distance moved showed a significant negative correlation with population size for males ($r = -0.724$, $p < 0.05$), but not for females ($r = 0.437$, $p > 0.10$; Figure 4.8).

4.4 - Discussion

4.4.1 - Population dynamics of woodmice: annual fluctuations - Population dynamics of *Apodemus sylvaticus* have been extensively studied in Britain, mostly in deciduous woodland (e.g. Ashby, 1967, Watts, 1969, Flowerdew, 1972, 1974, 1976b, Gurnell, 1978, 1981, Montgomery 1979, 1980). The results of these and other studies were reviewed by Flowerdew (1978, 1985, 1987) and Montgomery (1989a). The patterns can be summarized as follows.

1) Population densities usually fall in spring, are relativelly stable through early summer but start to increase by late summer and early autumn to reach an autumn or winter peak. Numbers often remain high through winter and start to decrease again in spring.

2) Food supply is probably a major influence on the peak densities reached in autumn / winter, but factors other than food supply also control the timing of increase and determine peak densities, especially density-dependent factors. It was suggested by Watts (1969) that the timing of the start of the population increase is density-dependent, with an earlier increase in years when summer population densities are low, so that autumn / winter numbers tend to be less variable than summer numbers. However, Flowerdew (1985) found that winter densities were probably more variable than proposed by Watts and Montgomery (1989a) found that less than one third of the variation in peak numbers was accounted for by density-dependent processes operating during the period of increase. Furthermore he did not find evidence of density-dependence in the timing of the start of the late summer increase.

3) The size of the spring decline is strongly influenced by overwinter food supply, but changes in the social and spatial structure of the population at the start of the breeding season (late winter or early spring) are likely to play a part as well. From this time of the year until early summer, juvenile survival is very poor probably as a result of aggression from overwintered males (Flowerdew, 1974, 1978; Gurnell, 1978). Thus numbers remain stable because survival of juveniles is poor, not because of any limitation on numbers born. Female territoriality at this time of the year may also limit recruitment of juveniles as suggested by Flowerdew (1985: 327). Indeed, the importance of female spacing behaviour in population regulation in woodmice has recently been emphazised by Montgomery *et al.* (1991).

4) In autumn, by the end of the breeding season, food supplies are often good; most overwintered males have died, the remaining ones are less aggressive towards juveniles and immigrants; female territoriality is reduced. As a result, survival of juveniles improve and the population grows to a peak.

5) In times of high numbers, populations of woodmice can show a density-dependent reduction in the proportion of reproductive females (Watts, 1969; Smal and Fairley, 1982) or even an early end to breeding (Watts, 1969; Montgomery, 1981). On the other hand, in years with a very good food supply, breeding may extend well into the winter (e.g. Smyth, 1966) and as a result density-dependent regulation may break down and populations continue to grow through the winter (e.g. Gurnell, 1981; Smal and Fairley, 1982).

The patterns found at the Corner Complex can be compared to the picture sketched above, point by point, as follows.

1) The pattern of seasonal fluctuation in numbers was consistent in most respects with patterns found previously for *A. sylvaticus*. Population sizes were low in spring in both years, and did not show any consistent increase until early summer. In both years

population increase started by late summer and peak numbers were found in October. The only point which differed from the previous studies was that in Corner Complex numbers decreased earlier than usual. There was a sharp fall between October and November and a quick overwinter decline by late winter in both years, as revealed by the low February population sizes. Thus, sustained high numbers in winter, as found in several previous studies, were not found in the present study.

2) Spring / early summer densities were indeed highly variable from year to year: intermediate in 1990, considerably higher in 1991, lowest in 1992. In contrast, autumn peak numbers were strikingly similar: estimated population sizes were 145.71 in October 1990 and 159.71 in October 1991 (four grids trapped in both occasions). Although my data are not suitable to test the hypothesis of density-dependent regulation of the autumn numbers, they are consistent with this hypothesis.

3) Generally, males had bigger home ranges and movements in spring and summer than in autumn and winter. Such a difference was not found in females. A high proportion of females was reproductive in the population in the spring and summer of both 1990 and 1991, and in the spring of 1992 as well. However, during most of spring and summer in both 1990 and 1991 juvenile recruitment was low, and juvenile survival was considerably lower than adult survival . The low juvenile recruitment in spite of active reproduction in spring / early summer was most dramatically illustrated by the June 1992 data. All females captured that month (five) were reproductive, yet juvenile recruitment was zero. The explanation of this apparent paradox is that juvenile recruitment and juvenile survival are unlikely to be independent parameters. An individual will count as a recruit only when it appears in the trappable population of independent individuals, seldom weighing less than 12g at the first capture. Whether it does so depends on its survival during the early, non-trappable weeks of its life. Therefore, the low juvenile recruitment in times when a high proportion of females was reproductive probably indicates a low survival of juveniles in the early stages of their lifes. Putting together all parameters, the pattern found for wood mouse populations in spring and summer is consistent with the ideas that adult males use large home ranges in the search for reproductive females, and that there is a considerable production of young individuals which nevertheless have very low survival in the early stages of their lives, probably due to competition with more successful adult individuals.

4) In autumn, male home ranges and movements were smaller than in spring and summer. Adult survival and the proportion of reproductive females were both high in the early phases of population increase in both years. Estimated juvenile survival was also very high in late summer / early autumn in 1991, but not in 1990. However, juvenile recruitment was very high by this time of the year in both years, and this pattern is likely to reflect an

increase in early juvenile survival as well (see previous paragraph). The population increase was significantly correlated with this increase in juvenile recruitment. Overall, the results were consistent with the idea that the late autumn/early summer population increase is due to sustained reproduction and improved juvenile survival, probably due to reduced interference from the adults.

5) In woodmice in Corner Complex breeding stopped in both winters and thus the annual pattern of population fluctuation was not overidden in either year. There was also evidence of a strong delayed density-dependence in the reduction of the proportion of reproductive females by late autumn in both years. It seems that this was an important factor in limiting peak numbers and in determining the timing of start of the population decline. Evidence of density-dependence during the decline phase was found also in the negative correlation between total survival in a given month and population density in the previous month, so that total survival was low by late autumn of both years. As total survival lumps together all age classes, this is not very informative of the processes going on within the population. However, this result may reflect a density-dependent reduction chiefly in adult survival, which may not have been detected due to the lower accuracy of P_{min} (used to estimate age class survival) as compared to Manly-Parr (used to estimate total survival). Indeed, among the age classes taken separately, adult survival showed the strongest (although non-significant) delayed negative correlation with population size. All considered, the strong density-dependent reduction in reproduction and probably adult survival as well seems to be one of the most distinctive features shown by the woodmice at Corner Complex when compared with the processes found in previous studies on this species.

It is also interesting to compare my results with Tanton's (1965, 1969) suggestion that population estimates for woodmice in summer are not reliable because trappability of this species is very low then. In Corner Complex, trappability was comparatively low (below 0.7) from July to October 1990 (Table 4.1), which might seem to support his hypothesis. However, as felling happened within this period it is impossible to separate the effect of season from a possible adverse effect of the felling process on trappability. Bank vole trappabilities were also low in July and September 1990, and woodmice trappabilities in 1991 were low only in spring, but not in summer. Thus, data obtained in the present study do not provide clear support for Tanton's suggestion.

4.4.2 - Differences between years and their effects on woodmice populations - Most points discussed in the previous Section apply to the whole study, but some marked differences are also evident when the first and the second year are compared. In 1991 the

population increase started earlier than in 1990, and high numbers were sustained for a much longer period, although peak numbers were similar and reached at a similar time. Thus, numbers increased earlier in the year when early summer population levels were higher. This result supports Montgomery's (1989a) contention that density-dependent control of the timing of autumn peak is not a constant feature in *A. sylvaticus* population dynamics as had been suggested by Watts (1969). As for the overwinter population decline, it was much sharper following 1991 than it had been following 1990, and numbers were still falling by the end of the study in June 1992. This final decline was apparently linked to an exacerbation of the common annual pattern: a complete failure in recruitment, in spite of considerable reproductive activity in the population in spring 1992.

The higher numbers in 1991 seemed to be at least partly due to better prospects for juveniles in that year than in 1990. Throughout the study, population size was significantly correlated with juvenile recruitment. Recruitment increased earlier in 1991 than in 1990, which explains the earlier population increase. Additionaly, juvenile survival was high for a longer period in 1991 than in 1990, which explains the high numbers being recorded for a longer period in 1991. Survival of adults and proportion of reproductive females, on the other hand, decreased faster in 1991 than in 1990. This is consistent with the suggestion of density-dependent variation of these parameters made above, so that sharper declines in adult survival and reproduction were to be expected in the year when numbers were slightly higher and sustained for much longer.

The differences observed between years can be attributed to variations in the seed crop. Data on inter-annual variation in production of Sitka spruce seeds in Hamsterley was available from the Forestry Commission seed store in Alice Holt Lodge, Hampshire. Such data do not allow fully quantitative estimates of seed production, but years at a given locality can be compared by the respective amounts of seed arriving from that locality to the seed store. As discussed in Chapter 1, although some of the Sitka seed is dropped by the autumn of the same year it is produced, most is dropped in the following spring. Thus the availability of seeds on the ground during most of the year is related to the production of seeds on the trees in the previous year. Keeping this in mind, the information on Hamsterley indicate that much more seed was available to rodents on the ground in 1991 than in 1990: "...1990 was a particularly good seed year in Sitka spruce (...) there were very large numbers of seed dispersed during the autumn of 1990 through to early spring of 1991 (...) the general level of seed production in 1988 and 1989 was lower than 1990 so the number of seeds on the ground during 1989 and 1990 would certainly be less" (C.J. Nixon, Forestry Commission, pers. comm.). "...1990 cone crops were best, 1991

marginally worse and 1989 the poorest." (Dr. P. Gosling, Forestry Commission, pers. comm.).

Studies on the food eaten by woodmice in a variety of habitats have established that seeds are a major component of their diet (Watts, 1968; Hansson, 1985) although the mice can turn largely to invertebrates if seeds are scarce either seasonally (Watts, 1968) or locally (Obrtel and Holisova, 1979; Zubaid and Gorman, 1991). Correspondingly, the dependence of woodmice population fluctuations on seed supplies is well established. For example, Gurnell (1981), working in oak woodland, found that woodmice were able to reach a population peak earlier and sustain high numbers for longer in a year following an autumn of good seed production. That seems to be the case also in 1991 in Corner Complex, as seed availability on the ground must have been better than in the previous year. However, as 1991's own crop started to be dropped by October, it was not good enough to break down density-dependent population regulation in woodmice; indeed, density-dependence in the timing of the end of reproduction seemed to be particularly strong in 1991 in this species.

4.4.3 - Population dynamics of bank voles - Fluctuations in bank vole populations have usually been categorized into two types: annual fluctuations found in the southern parts of the species' range and multiannual cycles found in Northern Fennoscandia (Alibhai and Gipps, 1985; Stenseth, 1985). British populations were included in the non-cyclic category by Alibhai and Gipps (1985). In most cases this is probably true, but there are a few apparent exceptions. Ashby (1967) claimed three to four year cycles for bank vole populations in the deciduous Houghall Wood near Durham, Northern England, although Alibhai and Gipps did not include his study as an example of multi-annual fluctuations. Southern and Lowe (1982) trapped bank vole populations in Wytham Woods, near Oxford, from 1948 to 1981 and suggested that until 1964 populations followed two and a half year cycles. The pattern later broke down and probably due to this inconsistency Southern and Lowe's study is quoted by Alibhai and Gipps (1985: 287, plus their Fig. 1) as an example of "non-cyclic fluctuations". Newson (1963) studied another population in Wytham Woods where the typical annual fluctuation was overidden by a sustained increase in numbers lasting more than one year. In my view, it not clear whether British bank vole populations may show multi-annual cycles in the same way as field voles.

Whether affected by cyclicity or not, what is clear is that the pattern of annual fluctuations in bank voles is certainly more variable than in woodmice, although average seasonal trends are roughly similar (Alibhai and Gipps, 1985). The average pattern in

"typical" years (i.e. years with spring decline) is peak densities in autumn, a quick decline through winter, a slower decline in spring and an increase starting in summer towards the autumn peak. In other years the spring decline may not happen and the population fluctuations are erratic (Alibhai and Gipps, 1985: Figs. 3 and 5, respectivelly).

Annual trapping in eighteen sites within Hamsterley Forest for three to four years between 1989 to 1992 failed to find evidence of cyclicity in bank voles populations in the forest as a whole (Chapter 3). Nevertheless, in Corner Complex between year differences were greater for bank voles than for woodmice. Although bank voles were more abundant in Corner Complex in 1991 than in 1990, just like woodmice, several additional between year differences were found in the former species but not in the later. First, seasonal fluctuations were very different: peak numbers were reached in August in 1990 and in December in 1991, i.e., the second year did not correspond to the average pattern for "typical" years described by Alibhai and Gipps (1985: Fig. 3). Second, adult survival was very poor during most of 1990, but very high during 1991 and towards the end of the study. Third, an inverse relationship between adult and juvenile survival was found only in the year of high numbers (1991), but not in the year of low numbers (1990). Fourth, juvenile recruitment was much higher in 1991 than in 1990. As discussed above for woodmice (Section 4.4.1), this last pattern probably reflected an improvement in early juvenile survival, given that reproductive activity in the two years was similar. Thus the "typical" annual fluctuation in 1990 seems to have given place in 1991 to a long, steady population increase until the end of reproductive season, followed by sustained high numbers due to high survival overwinter and until spring 1992. The pattern of variation in numbers looks strikingly similar to one found by Newson (1963) in Wytham Woods: a nearly continuous population growth over two years, with only a slight spring decline in the start of the second year.

Arguably, the apparent continuous growth of bank vole populations in Corner Complex through the winter 1991-92 could have been just an artefact of the three month gap in trapping between March and June 1992. In this hypothesis, a marked spring decline would have happened after all, but it would have gone undetected because of the trapping gap. High numbers in June 1992 would represent a return to (rather than sustained) high population levels, due to recruitment towards the end of the gap. Recruitment data do not seem to support this hypothesis, because recruitment was very low in June 1992 (Figure 4.6). Additionally, only four out of 28 bank voles captured in that month were subadults, which could arguably also reflect recent recruitment. It seems that a quick recovery due to intense recruitment cannot explain the high numbers in June 1992, and therefore any spring decline in 1991-92, if it happened at all, was very slight.

A marked difference between Newson's results and mine is that he attributed the anomalous population increase to winter breeding but I found evidence that breeding stopped (although very late) in the winter of 1991-92: none of six adult females was reproductive in February 1992. Due to this small sample size, I can only suggest but not test the hypothesis that an overall trend of population increase spanning more than one year (as found by Newson) is not necessarily dependent on winter breeding, provided that the interruption of breeding is short and survival is high. In Corner Complex, bank vole adult survival was indeed high until March 1992, although estimates are not available later in the spring.

The relationship between population size and seed supplies is not likely to be as straightforward for bank voles as for woodmice in Corner Complex, for two reasons. First, bank voles' diet is usually more varied. Seeds are often less important, and bank voles use a greater variety of alternative food sources, especially green leaves, fungi, berries, lichens and bark (Watts, 1968; Flowerdew and Gardner, 1978; Smal and Fairley, 1980; Hansson, 1985). Second, as hinted in Chapter 3 and discussed more fully in the next two Chapters, the high abundance of bank voles in Corner Complex in 1992 was concentrated in a single grid, the clear-felling Corner 2. The case of this individual grid will be discussed in next Chapter. As a more general remark, patterns at the level of the population of the whole Corner Complex were generally clearer for woodmice than for bank voles. This was partially due to two non-independent factors: (1) bank voles moved less often between grids than woodmice (Section 4.3.4) and (2) bank voles are more habitat-specialist than woodmice in general (Chapter 3) and in Corner Complex in particular (Chapter 6). For these two reasons the large spatial scale approach applied better to the latter species than to the former.

4.4.4 - Home ranges and their relationship with population dynamics - The estimates of home range areas in Corner Complex (Tables 4.5 and 4.6) can be compared with previous studies on the same species using the Minimum Convex Polygon, keeping in mind that some authors published their results in m^2 and I presented mine in hectares (1 ha = 10,000 m^2). The areas I found were bigger than most previous trap-based studies, especially for woodmice (compare for example with Wolton and Flowerdew, 1985: Tables 2 and 3). Home range estimates based on radio-tracking have often resulted in values higher than my corresponding estimates, but it is well established that radio-tracking yelds higher estimates than comparable trap-based studies (Wolton, 1985; Attuquayefio *et al.*, 1986). Even within the set of trap-revealed home ranges, detailed numerical comparisons are not warranted because home range estimates are demonstrably dependent on trap

spacing, which varies among studies (Gurnell and Gipps, 1989). However, the comparisons suggest that home ranges in Corner Complex were bigger than average values for the respective species, especially in the case of woodmice.

Both home range areas and average distances moved were bigger for woodmice than for bank voles in Corner Complex. Most previous studies in a variety of habitats have also found this difference between the two species (Brown, 1956b, 1966, Bergstedt, 1966, Crawley, 1969, Wolton and Flowerdew, 1985). Exceptions were Kikkawa, 1964 (who found inconclusive results) and Smal and Fairley (1982) who found bigger home ranges for bank voles than for woodmice in an oak-yew woodland in Ireland.

Within each species, home ranges and movements are consistently bigger for males than for females (e.g. Brown 1956b, 1969, Miller, 1958, Bergstedt, 1966, Montgomery, 1979, Wolton, 1985; Attuquayefio *et al.*, 1986; present study). However, several studies have found this difference only in the early reproductive season (spring / summer) when male home ranges are much bigger than in autumn / winter (e.g. Kikkawa, 1964; Crawley, 1969, Randolph, 1977; Cody 1982 quoted by Wolton and Flowerdew, 1985; Attuquayefio *et al.*, 1986). By the end of the reproductive season and in winter, male and female home ranges may differ little in either species. This pattern is quite evident in Cody's (1982) data (quoted by Wolton and Flowerdew, 1985, their Tables 2 and 3). In the present study there was evidence for such a pattern in both species, but there were some considerable between year differences, which are probably due to the between year differences in population dynamics (Sections 4.4.1 to 4.4.3). For both species a significant negative correlation was found between actual population sizes and male home ranges and / or distances moved. For example, woodmice male home ranges were much larger in summer 1990 than in summer 1991, which seems to be associated with the earlier start of population increase in 1991. Distances moved by male bank voles were shorter from summer 1991 onwards, the period when numbers of this species were highest (distances moved are probably, although not necessarily, correlated with home range area). Thus, it seems that for both species male home range areas varied according to season if the population fluctuation followed its usual seasonal pattern, but they reflected actual numbers rather than season if the usual pattern was not followed. As noted by Wolton and Flowerdew (1985), patterns of spatial organization in woodmice and bank voles appear to be remarkably similar, in spite of their phylogenetic and morphological differences. In both species, in the early breeding season, males considerably increase the size of their ranges, while females increase theirs to a smaller extent, if at all, and may become territorial.

In the present study, the relationship between spatial patterns and population regulation in bank voles cannot be satisfactorily analysed, due to the marked differences

between years in the population dynamics of this species. However, seasonal variation of spatial patterns in woodmice can be related to existing spatial models and to how they affect population regulation. Ostfeld (1990) reviewed the evidence on territoriality by small mammals, proposing that females hold territories in spring and summer which provide food enough for their litters, provided that the quality and patchy distribution of the food make territories worth defending. Males, by their turn, distribute themselves spatially in order to maximize access to females while excluding competing males. The larger home ranges of males in spring and summer allow their home ranges to overlap several female home ranges. This model seems to be roughly consistent with the spatial structure of woodmice populations as reviewed by Wolton and Flowerdew (1985). Such spatial structure, in turn, is one of the factors involved in the mechanism of population regulation in woodmice as discussed in Section 4.4.1. Making allowance for between year differences in the seasonal variation of home ranges, which seem to be related to the between year differences in population fluctuations, the spatial patterns I found for woodmice in the Corner Complex were consistent with the ones described by Wolton and Flowerdew and put into a wider context by Ostfeld. Therefore, they provide additional evidence that the process of population regulation of woodmice in Corner Complex was mostly consistent with the views summarized by Flowerdew (1985) and Montgomery (1989a).

4.4.5 - Woodmice in a Sitka successional mosaic: usual population dynamics in an unusual study area - At least three major differences were observed between woodmouse population dynamics in Corner Complex and the patterns found elsewhere by previous workers. All three were observed at a similar time of the year (late autumn) and may well be closely related to each other. Numbers started to fall earlier in autumn in Corner Complex than in most previous studies; overall survival suffered a density-dependent reduction by late autumn, apparently chiefly the result of reduced adult survival; and reproduction was also severely reduced by late autumn, again in a density-dependent way. All three pieces of evidence suggest that there was strong density-dependent regulation of wood mouse population size in Corner Complex as early as late autumn, contrary to Montgomery's (1989a) view that density-dependent factors usually explain little of the decline phase in woodmice populations.

It is tempting to try to find a single hypothesis to explain this early, density-dependent decline. One reason may be that many Sitka seeds are not dropped within the same year as they are produced. As a consequence, late autumn food supply in Sitka might be less plentiful than in a forest where all seed is dropped in the year it is produced, as

happens in deciduous woodland where most woodmice population studies were carried out. As a second, non-exclusive hypothesis, it can be argued that density-dependence would be felt more severely in Sitka because this habitat is, as a whole, suboptimal as far as food supplies are concerned. This condition has been hypothezised for a Norway spruce (*Picea abies*) monoculture in Czechoslovakia by Holisova and Obrtel (1980). Their conclusion was based on the scarcity of ground vegetation (which would provide alternative food sources) under Norway spruce, plus the unusually high proportion of invertebrates found in the diet of woodmice in their study area (Obrtel and Holisova, 1979). Woodmice would have to feed on invertebrates in habitats where seed supply is poor, a suggestion later corroborated by Montgomery and Montgomery (1990) in conifer plantations in Ireland and by Zubaid and Gorman (1991) on a sand dune in Scotland. Data on diet of the Corner Complex woodmice are not available at present, but the scarcity of ground vegetation under mature Sitka spruce and recent clear-fellings was clearly demonstrated by the habitat analysis described in Chapter 3. The large woodmice home range areas in Corner Complex provide further support for the hypothesis of scarce food resources; home range areas of woodmice are inversely correlated with habitat quality (Attuquayefio *et al.*, 1986).

However, it is interesting to note that, apart from this difference in timing and nature of the decline, all other population processes for woodmice were remarkably similar to those in other habitats, mostly deciduous woodland, as found in previous studies (Section 4.4.1). In most cases those studies were made deliberately in an homogeneous habitat, habitat heterogeneity being a possible complicating factor in population dynamics. In the present study the habitat was known to be heterogeneous at the start. Yet, most features of wood mouse population dynamics as described by previous investigators were easily recognizable. Therefore, habitat homogeneity is not a necessary condition for the mechanisms of population regulation in woodmice discussed in Section 4.4.1 to operate. On the contrary, habitat heterogeneity - even if more subtle than in Corner Complex - may be an important component of the mechanism of regulation. This possibility has been discussed previously for field voles (Hansson, 1977), bank voles (Stenseth, 1985) and more recently for woodmice (Montgomery, 1989b; Montgomery *et al.*, 1991). The role of habitat heterogeneity in population regulation within the Corner Complex is discussed in Chapter 6.

CHAPTER 5

RODENT POPULATIONS IN A HABITAT MOSAIC PRODUCED BY FELLING: II - HABITAT CHANGES ASSOCIATED WITH CLEAR-FELLING AND THEIR EFFECTS ON THE LOCAL ABUNDANCES OF RODENTS

5.1 - Introduction

5.1.1 - Clear-felling, tree brashings, and rodent populations: a field experiment on the effects of a drastic habitat change - Strictly speaking, the clear-felling of a forest is not an event in natural forest succession; it most closely resembles the effects of damage from wind-throw in which the successional process would start afterwards. Nevertheless, clear-felling is one of the quickest and most extensive "experimental" changes a forest habitat can experience. The process itself, which involves cutting and removing all trees with heavy machinery, is potentially hazardous to rodents. Considering both this fact and the close relationship often found between abundance of a particular rodent species and structural characteristics of the habitat (e.g., Chapter 3), one would expect clear-felling to be a time when rodent communities would suffer especially quick and dramatic changes (Kirkland, 1977, 1990, Morrison and Anthony, 1989).

The magnitude and direction of the changes in rodent communities may also be linked to specific forestry practices for felling. For example, after the trees are cut, the trunks of all commercially valuable trees are stripped of their branches and taken away from the felled area. The branches, pieces of trees, and those trees which are not comercially valuable (together forming what hereafter are called "tree brashings"), may simply be left to decompose *in situ*, or they may be removed, usually by controlled burning. In Forestry Commission plantations it has been more common recently to leave the brashings *in situ*; this is partly because of the cost involved in removing them and partly because they reduce the growth of plants which may compete with tree seedlings (Gibson, 1989).

The two alternative practices markedly affect the habitats created thereby for rodents. Colonization by ground vegetation should be quicker if the brashings are removed, which might improve the habitat for rodents. On the other hand, the tree brashings are almost the only kind of ground cover available in recent clear-fellings; their removal should increase the vulnerability of the rodents to predators, especially birds of prey. Indeed, belts of cleared ground were used by Muñoz and Murúa (1990) in a

plantation of pine (*Pinus radiata*) in Chile to increase the efficiency of predation by barn owls (*Tyto alba*) on small rodents. Arguably, the removal of brashings could also improve the efficiency of mustelid predators in localizing their prey, as they orient primarily by sight, and only secondarily by smell (King, 1985). In Hamsterley, there are short-eared owls, *Asio flammeus*, and tawny owls, *Strix aluco* (Gibson, 1989; B. Walker, pers. comm.), and during the present study I made four captures of weasels (*Mustela nivalis*) in Longworth traps, plus twelve sightings of mustelids (weasels and stoats, *M. erminea*). Thus, predators were available in the study area to benefit from any increased vulnerability of the rodent populations. However, it should be noted that if the anti-predator defences of different rodent species depend on ground cover to different extents, the removal of brashings could make the habitat unsuitable for some rodent species only, and not for others.

The present Chapter reports the results of two field experiments on the effects of clear-felling of a part of a Sitka spruce plantation in Corner Complex (Hamsterley Forest) on the local rodent populations. The first field experiment was the clear-felling itself, of a block of mature Sitka spruce. The second involved the removal of all the tree brashings from recent clear-fellings. In both cases, rodent populations were trapped within the experimental sites before and after the manipulation. Additionally, simultaneous rodent trapping was carried out in control (i.e. unmanipulated) sites. The results of the experiments were evaluated by comparing rodent abundances in the experimental areas and in the controls, to try to separate the effects of the manipulations from the seasonal or inter-annual fluctuations in density of each rodent population (Chapter 4). Additionally, pre-experimental similarity between control and experimental areas, as well as between experimental replicates, was also tested whenever possible, following Hurlbert (1984).

5.1.2 - Testing predicted effects of the habitat changes - Hairston (1989) emphasizes the need for formulating explicity the hypotheses being tested in ecological experiments, preferably by making predictions which the outcome of the experiment could either confirm or reject. Although in most previous studies of clear-felling (reviewed by Kirkland, 1990) an increase in overall small mammal population densities occurred, the patterns were significantly influenced by geographical locality and characteristics of the forest being felled (Parker 1989). Thus, predictions of the results of the experiments should be based on patterns found in a particular locality - in the present case on those in Sitka spruce clear-fellings within Hamsterley Forest (see Chapter 3; Vadher, 1990). Such predictions, for the two experiments described above, are as follows.

(1) Effects of clear-felling: overall rodent population densities would remain similar to the levels found in the mature forest before felling. Woodmice would become the dominant rodent species in the clear-fellings; bank voles, even if present in abundance in the mature forest, would become scarcer than woodmice in the new habitat.

(2) Effects of the removal of tree-brashings from the clear-fellings: this manipulation would severely reduce the population levels of bank voles, as the abundance of this species usually is dependent on ground cover (Chapter 3) and in particular can be correlated with the amount of slash left in reforestations (Jensen, 1984). Woodmice would be less affected by the manipulation than bank voles. As a consequence, dominance of woodmice in the clear-fellings would be further increased, possibly forming single-species "communities".

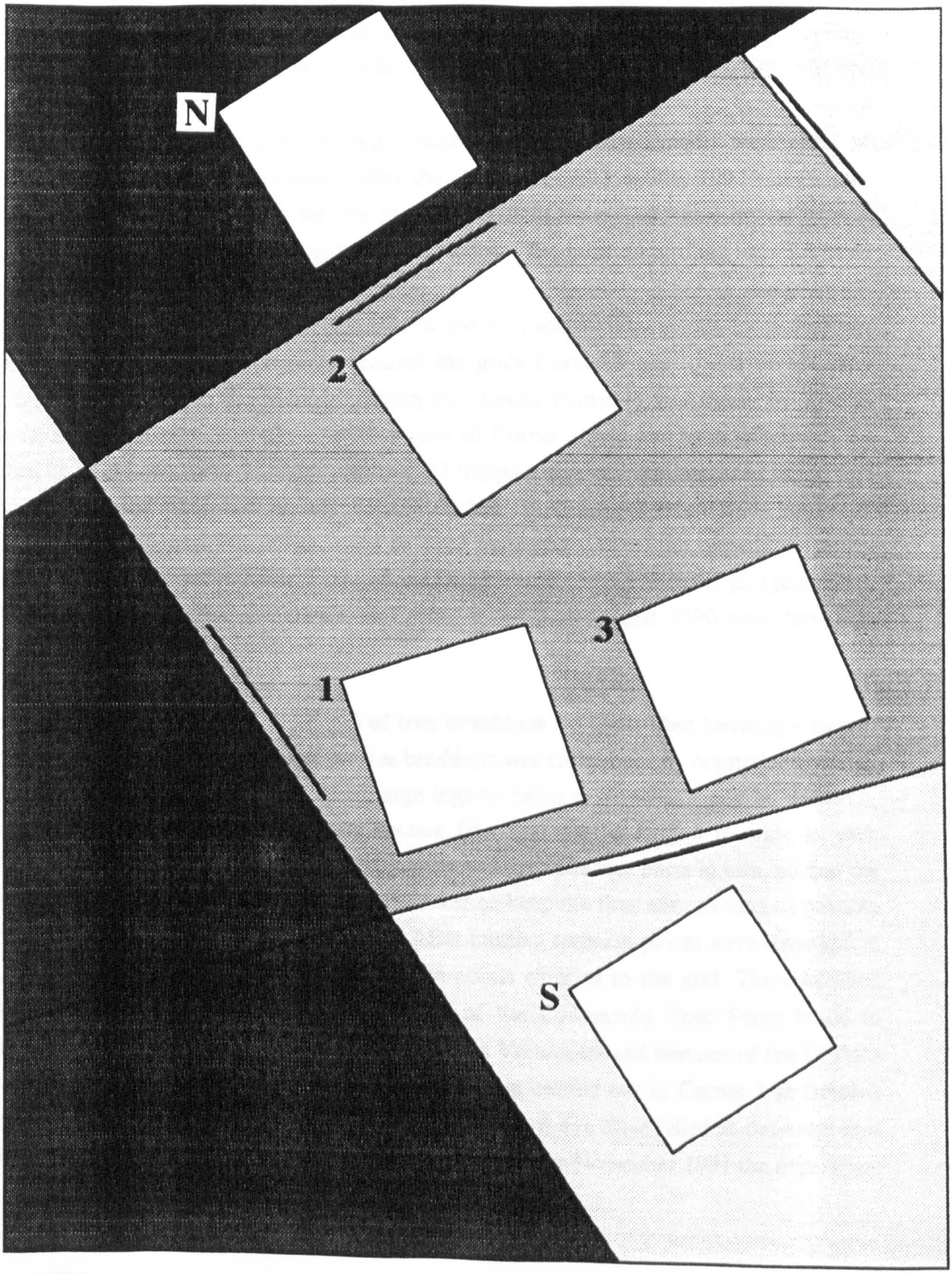
Besides testing these predictions, the present study aimed to investigate whether the process of felling itself causes rapid changes in rodent abundances or whether the changes take place gradually after felling is completed, as rodent communities are constrained by the new habitat.

5.2 - Methods

5.2.1 - Trapping design and trapping programme - Within a Sitka spruce block of six hectares, planted in 1946 and scheduled for felling in the summer of 1990, two standard grids (Corner 1 and Corner 2) were trapped from March, 1990 onwards. These two sites initially were mature forest but their trees were cut and removed in July-August 1990. Two control sites (i.e. sites adjacent to the felled block, but which did not change successional stage during the study) were trapped from May, 1990 onwards. The two controls were Corner North, a mature plantation (also planted 1946) not scheduled for felling, and Corner South, an area clear-felled in 1989. After the felling, all trapping points within Corner 1 and 2 were remarked in the original places with the help of reference points external to the grids. In September 1990, just after the felling was completed, an additional grid was marked within the area that had just been felled (Corner 3). The positions of the five grids and habitat types within and around the Corner Complex are shown in Figure 5.1. Year of planting and soil characteristics of each grid were presented earlier, in Table 3.1, Chapter 3.

A standard trapping session was carried out in each month (except in January of 1991 and 1992) in all grids from 1990 until March 1992, plus an additional early summer trapping session in June 1992. However, Corner 1 and 2 could not be trapped in July

FIGURE 5.1. Position of the five standard grids trapped within Corner Complex. Within the mature plantation felled in July-August 1990, trapping started in grids 1 and 2 before felling, and in grid 3 in September 1990. Grids North (N) and South (S) were respectivelly a mature plantation and a clear-felling throughout the study (May 1990-June 1992). Lines parallel to the edges of the felled block show the position of the additional trapping lines in grassy verges (trapped in May and August, 1990).



1990, due to the tree felling activities and Corner 1 and 3 could not be trapped in October 1990 and October-November 1991 respectively, because of brash removal for the field experiment. In December 1990 and February 1991, because deep snow hindered trapping sessions, valid data were obtained only for the experimental grids (Corner 1 to 3) but not for the controls.

In addition to the grid trapping described above, 80 trap nights were spent in trapping lines in grassy verges surrounding the Corner Complex in May 1990 and another 80 in August 1990, to check for the presence of field voles (*Microtus agrestis*) as a potential invader of the area during the time of felling. The position of these lines is shown in Figure 5.1.

The felling started on the east side of the six-hectare Sitka spruce block in June, 1990. In July, the felling machines reached the grids Corner 1 and 2, and no trapping could be carried out in the two grids during that month. However, in August the process of felling was discontinued again. By this time all Corner 1 grid had been felled, but the trees had not been removed from one half; 20 trapping points were remarked in the half from which the trees had already been extracted. In Corner 2 most trees were still standing, and 45 trapping points could be used in August: 30 of the original 49 points which were still within standing forest, plus 15 which were remarked in the part just felled. The estimates of rodent abundances in Corner 1 and 2 in August 1990 were based on these incomplete grids.

5.2.2 - A field experiment: removal of tree brashings by controlled burning - In two grids, Corner 1 and 3, removal of the tree brashings was carried out by controlled burning. In each grid, all pieces of trees, from large logs to twigs as small as could be gathered, were removed from an area of one hectare (the grid plus a strip 5 m wide in each direction). The brashings were gathered in piles and each pile was burnt in turn, so that the fire would not get out of control. Care was taken to keep the fires alive as long as possible in order to burn out each pile completely. After burning trapping points were remarked in the original places with the help of reference points external to the grid. The controlled burning was carried out with the assistance of the Community Task Force based in Hamsterley. The Durham University Conservation Volunteers and inmates of the Durham Prison provided extra help. The first experiment was carried out in Corner 1 in October 1990, Corner 2 remaining as a control, i.e., an adjacent site clear-felled at the same time but which did not have the brashings removed. In October-November 1991 the experiment was repeated in Corner 3, Corner 2 again being the control.

5.2.3 - Estimates of rodent abundances in each grid and comparisons between grids - As the rodents captured in each grid did not form independent populations (Section 4.3.4), throughout this Chapter "population" refers to the rodents inhabiting the whole Corner Complex, and "subpopulation" refers to those found in a single grid. Manly-Parr subroutines for estimation of population sizes, survival and trappability (as used in Chapter 4) were not applied to the subpopulations for two reasons, as follows. First, sample sizes often were not large enough. Second, I was especially concerned with fluxes of individuals between grids, which might be seasonally reversed (see next Chapter). A method was needed therefore which treated an individual which had moved from grid A to B by month t, but returned later, as absent from A at t. Both Manly-Parr or the simple technique often used for small sample sizes, the MNA (Minimum Number Alive; Krebs, 1966) would have counted the individual as present in A at month t if it returned there at a later date. Thus, subpopulation sizes for individual grids at month t were estimated simply by the number of different individuals captured in each grid at t. This estimate is likely to be negatively biased; nevertheless, provided that a similar bias applies to all grids, this estimator should be useful for comparisons between subpopulations.

When comparing the number of individuals caught in different grids, I used paired-sample tests in order to separate seasonal variations in numbers (which occur in all grids) from the inter-grid variations which were being tested. In several cases the available sample sizes (i.e. number of months) were too small to assess the normality of the distributions, which is an assumption of the paired Student's t-tests often used for this kind of comparison. Thus, I opted for a cautious approach and tested differences between grids using the non-parametric analogue of the paired t-test, the Wilcoxon signed ranks test. This test is less powerful than the t-test, but on the other hand it does not assume normality of the distributions (Zar, 1984).

5.2.4 - Testing the effects of the removal of brashings: comparisons between rodent spatial distributions - The removal of tree brashings was performed only within the grids plus the 5 m strip around them. Thus it is conceivable that animals from the surrounding areas could have invaded the grids and inflated the counts of animals within each grid; this is the so-called "edge effect" (Smith *et al.*, 1975; Flowerdew, 1976; Tanaka, 1980). The edge effect is a common problem when estimating population densities, but provided that a grid covers only part of the area of the single habitat it samples, grid-based estimates of population sizes can be used as an index to population densities (Section 4.2.2). If however the habitats within and around the grid differ sharply, such an index could be misleading. It might happen in such a case that animals caught within the grid come

mostly, or entirely, from the habitat surrounding the grid; in this case the rodent populations caught in the grid would certainly not be representative of the habitat within it. Additionally, if different rodent species show edge effects to different degrees, the relative abundances of the species within the community could be grossly misrepresented by captures within the grid.

To correct for this bias in the grids where brashings were removed, I tried to estimate edge effect by comparing the observed and expected frequencies of captures in the outer and inner traps with Chi-square tests. This method is based on Schroeder's (1981) method, which assumes that an edge effect would inflate the number of captures in the outer traps more than in the inner ones and detects any effect by comparing the trapping success of traps located in different positions of a grid. In the present study, the expected proportions were 24/49 of the captures in the 24 outer traps, and 25/49 of the captures in the 25 inner ones. All comparisons were carried out with contingency Chi-square tests with one degree of freedom, using Yates' correction for continuity. When interpreting the results, care was taken with the assymetrical implications of two possible patterns, as follows. If captures of a species were concentrated along the edges of a grid, there was evidence of edge effect due to dependence on shelter. On the other hand, if a pattern of captures was evenly distributed the species did not depend on shelter, but this does not necessarily mean that there was no edge effect. If animals from the surroundings move considerable distances in relation to the size of the grid and they do not depend on shelter, they could easily move towards the center of the grid as well, to an extent that would make the pattern of captures concentrated in the edges vanish completely.

5.3 - Results

5.3.1 - The effects of clear-felling on rodent abundances - The numbers of different individuals of each rodent species caught each month before felling in the two experimental grids Corner 1 and Corner 2 are shown in Tables 5.1 and 5.2, together with the levels recorded in the two control grids, Corner North (mature) and Corner South (felled). *A. sylvaticus* was found in all grids, and *C. glareolus* was absent only from the old clear-felling control Corner South.

During the four months before felling, woodmice were significantly more abundant in Corner 2 than in Corner 1; a similar difference was significant in bank vole abundance only at the $p = 0.072$ level (Table 5.3). Thus, there was evidence of some pre-felling heterogeneity amongst these two experimental grids. No statistical comparison was

TABLE 5.1. Monthly variations in the abundance of woodmice (*Apodemus sylvaticus*) in each grid of the Corner Complex. Values are numbers of different individuals actually caught.

Time		Co1(M-F)	Co2(M-F)	Co3(F)	CoS(F)	CoN(M)
	Mar	**1**	**10**	-	-	-
	Apr	**4**	**13**	-	-	-
	May	**5**	**11**	-	8	9
	Jun	**3**	**9**	-	9	7
1990	Jul	Felling	Felling	-	3	5
	Aug	3*	10*	-	3	6
	Sep	19	7	14	3	9
	Oct	BrashRem	24	23	23	22
	Nov	*30*	18	29	13	13
	Dec	*22*	8	9	-	-
	Feb	*3*	10	10	-	-
	Mar	*11*	13	9	3	18
	Apr	*5*	3	6	6	6
	May	*3*	9	8	6	11
	Jun	*2*	14	7	6	31
1991	Jul	*14*	26	20	16	33
	Aug	*14*	25	22	18	32
	Sep	*12*	27	23	30	28
	Oct	*32*	42	BrashRem	44	27
	Nov	*22*	23	BrashRem	29	18
	Dec	*15*	18	*6*	23	12
	Feb	*2*	6	*3*	5	3
1992	Mar	*4*	5	*9*	5	3
	Jun	*4*	2	*3*	0	4

Note. Periods when either clear-felling or the experimental removal of tree brashings was taking place ("Felling" and "BrashRem" respectively) are indicated. Successional stages of the grids are: M, mature; F, clear-felling. Values for mature grids are shown in **bold**; clear-fellings in standard; experimental (brash removed) plots *italics*. Asterisks (*) for August, 1990 indicate samplings based on incomplete grids in Corner 1 and 2 at the time of felling (see text).

TABLE 5.2. Monthly variations in the abundance of bank voles (*Clethrionomys glareolus*) and field voles (*Microtus agrestis*, numbers in superscript) in each grid of the Corner Complex. Values are numbers of different individuals actually caught. All symbols as in Table 5.1.

Time		Co1(M-F)	Co2(M-F)	Co3(F)	CoS(F)	CoN(M)
	Mar	0	2	-	-	-
	Apr	0	2	-	-	-
	May	1	1	-	0	1
	Jun	1	5	-	0	3
1990	Jul	Felling	Felling	-	0	6
	Aug	1*	10*	-	0	11
	Sep	2	7	1	0^{1}	5
	Oct	BrashRem	8	0	0^{3}	11
	Nov	*2*	3	0	0^{2}	5
	Dec	*1*	2	1	-	-
	Feb	*0*	5	2	-	-
	Mar	*0*	7	1	0^{3}	10
	Apr	*0*	6	3	0	2
	May	*1*	7	1	0	7
1991	Jun	*1*	3	1	0	9
	Jul	*4*	5	0	0	9
	Aug	*3*	3	2	0	16
	Sep	*1*	5	3	0	12
	Oct	*2*	8	BrashRem	0	12
	Nov	*1*	12	BrashRem	1	7
	Dec	*1*	21	*0*	1	3
	Feb	*2*	19	*0*	1	3
1992	Mar	*4*	22	*0*	1	2
	Jun	*1*	20	0^{1}	1	8

TABLE 5.3. Effects of clear-felling and of removal of tree brashings on the abundance of woodmice and bank voles in different grids within the Corner Complex (data from Tables 5.1 and 5.2). Statistics shown are values of z, the normal approximation to Wilcoxon signed ranks test's V, and their probabilities (p). Direction of differences are given by the sign of z's: positive and negative z's indicate that numbers are higher in the first or in the second grid quoted, respectively. Symbols are: n, sample sizes (months); *, significant ($p < 0.05$); **, highly significant ($p < 0.01$).

Effects being tested	Comparison	n	Woodmice		Bank voles	
			z	p	z	p
EFFECTS OF CLEAR-FELLING						
Homogeneity of replicates before the experiment	1 x 2, before felling of both	4	1.826	< 0.05 *	1.461	0.072
Effects of felling: experimental x control	2 x N, after felling of 2	16	1.189	0.117	1.189	0.117
	As above, but until Sep/Oct 1991 only	10/11	-0.866	0.193	-1.067	0.143
	As above, but from Oct/Nov 1991 only	6/5	1.992	< 0.05 *	2.023	< 0.05 *
EFFECTS OF REMOVAL OF BRASHINGS						
Homogeneity between experimental and control before the experiment	1 x 2, before brash removal in 1	5	-0.674	0.250	-2.023	< 0.05 *
	3 x 2, before brash removal in 3	12	-0.552	0.291	-3.059	< 0.01 **
Effects of brash removal: experimental x control	1 x 2, after brash removal in 1	16	-0.517	0.303	-3.516	< 0.001 **
	As above, but excluding autumn 1990	14	-2.767	< 0.01 **		
	3 x 2, after brash removal in 3	4	-0.730	0.233	-1.826	< 0.05 *

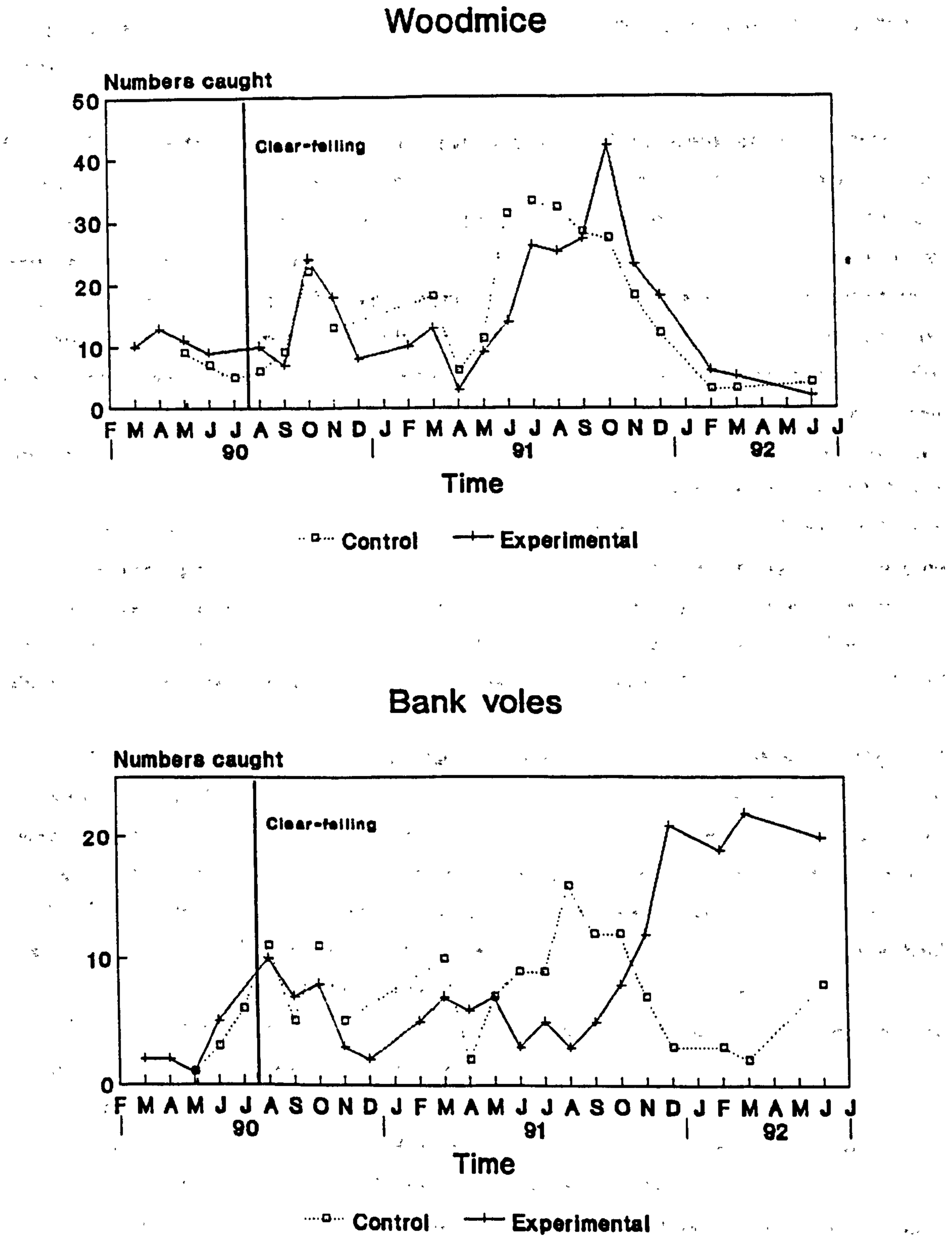
possible between rodent abundances in the mature control Corner North and in Corner 1 or Corner 2 before felling. However, the numbers of woodmice and especially bank voles in Corner North were more similar to Corner 2 than to Corner 1 in this period (Tables 5.1 and 5.2). Therefore, given the pre-felling heterogeneity between the two experimental grids, I chose to analyse the effects of felling by comparing Corner North (the mature control) only with Corner 2, the most similar of the experimentals.

The effects of clear-felling on the rodent populations are shown in Figure 5.2, which compares abundances of each species of rodent in Corner 2 and Corner North before, during and after felling. Considering that in August 1990 only 45 instead of 49 traps were placed in Corner 2, there was no obvious reduction in the abundance of either rodent species in Corner 2 compared to previous months or to the mature control grid (see Figure 5.2). After felling was completed and until the end of the study in June 1992, the abundances of both rodent species were not significantly different between Corner 2 and the mature control Corner North (Table 5.3). However, some finer-scale pattern was apparent if this period was divided in two instead of being considered as a whole. In the first year after felling (until September for woodmice and October 1991 for bank voles), variation in numbers of both rodent species followed parallel seasonal trends in Corner North and Corner 2 (Figure 5.2); abundances were higher in the mature forest control than in the clear-felling in most cases, although no significant difference could be established for either species (Table 5.3). However, from October-November 1991 onwards, the pattern was reversed: both woodmice and bank voles became more abundant, and significantly so, in the clear-felling Corner 2 than in Corner North (Table 5.3). Wood mouse abundances in both grids still followed parallel seasonal fluctuations, but bank vole numbers in Corner North reached a peak in late summer-early autumn in 1991 and fell sharply thereafter, whilst numbers in Corner 2 peaked later (March 1992) and were still high by the end of the study in June (Figure 5.2).

The three new clear-fellings were also found to differ from the older control clear-felling (Corner South) in terms of the presence of bank voles, which were found in Corner 1 , 2 and 3 from just after felling, but were completely absent from Corner South until November 1991 (Table 5.2). On the other hand, all but one of the field voles caught within Corner Complex were captured in Corner South and not in the newer clear-fellings (Table 5.2). Thus, the new clear-fellings apparently had not converged by the end of the study to the same community composition as shown by Corner South, and for this reason the latter grid was not used as a clear-felled control in comparisons as originally planned.

During trapping in the grassy verges around the Corner Complex in May 1990, 3 field voles were captured in the lines, but none was ever captured elsewhere. In August

FIGURE 5.2. Effects of clear-felling on rodent abundances: numbers of different individual woodmice (top) and bank voles (bottom) caught in the control grid Corner North (a mature Sitka spruce plantation) and in the experimental grid Corner 2, where trees were felled in July-August 1990 (time of clear felling is indicated as a vertical line).



1990 no field vole was caught among 7 rodents captured in the lines. The populations of field voles were apparently low in Corner Complex just as they were all around Hamsterley at that time (Chapter 3), and thus this species was scarcely available to invade the new habitat after clear-felling was finished.

5.3.2 - The effects of the removal of brashings on rodent abundances - Figure 5.3 shows the variations in the abundance of woodmice and bank voles in the experimental grid Corner 1 and the control Corner 2 before and after the tree brashings were removed from the former grid in October 1990. Before the manipulation, both species were more abundant in Corner 2 than in Corner 1 in most months (a significant difference was found for bank voles, although not for woodmice; Table 5.3). These results provide evidence of some heterogeneity between the two sites before the brashings were removed. Thus the validity of Corner 2 as a control to Corner 1 is open to question and consequently the comparisons should be interpreted with care. Having said that, from the first trapping after the removal of brashings (November 1990) until the end of the study in June 1992, the abundance of bank voles was much higher in Corner 2 than in Corner 1 (Figure 5.3); the difference was highly significant (Table 5.3). There was a short-lived "pulse" of abundance of woodmice in Corner 1 in the two months imediately after the brashings were burned, i.e., November and December 1990, but thereafter the species was significantly less abundant in the experimental grid Corner 1 than in the control Corner 2 (Figure 5.3 and Table 5.3).

The effects of the replication of the experimental removal of brashings, in Corner 3 in October-November 1991, are shown in Figure 5.4. Before the experiment, bank voles were again significantly more abundant in the control Corner 2 than in Corner 3, although no significant difference was found between the abundance of woodmice in the two grids (Table 5.3). Thus the same reservations which apply to Corner 2 as a control to Corner 1, also apply to Corner 2 as a control to Corner 3. After the brashings were removed bank voles remained significantly more abundant in Corner 2 than in Corner 3 (Table 5.3), but the difference was more marked than before the experiment: bank voles became more abundant in Corner 2 than in any other grid, while none was caught in Corner 3 in the same period (Table 5.2). The removal of brashings produced no obvious effect on the abundance of woodmice: just as before the manipulation, no significant difference was found between the numbers of this species in the two grids (Table 5.3). In contrast to what had happened in Corner 1 in the previous year, no short-lived "pulse" of abundance

FIGURE 5.3. Effects of removal of tree brashings from clear-fellings on the abundances of rodents: first replicate. Graphs show the numbers of different individual woodmice (top) and bank voles (bottom) caught in the control grid Corner 2 and in the experimental grid Corner 1. Both sites were felled in July-August 1990, but brashings were removed from Corner 1 only, in October 1990 (time of removal of the brashings is indicated as a vertical line).

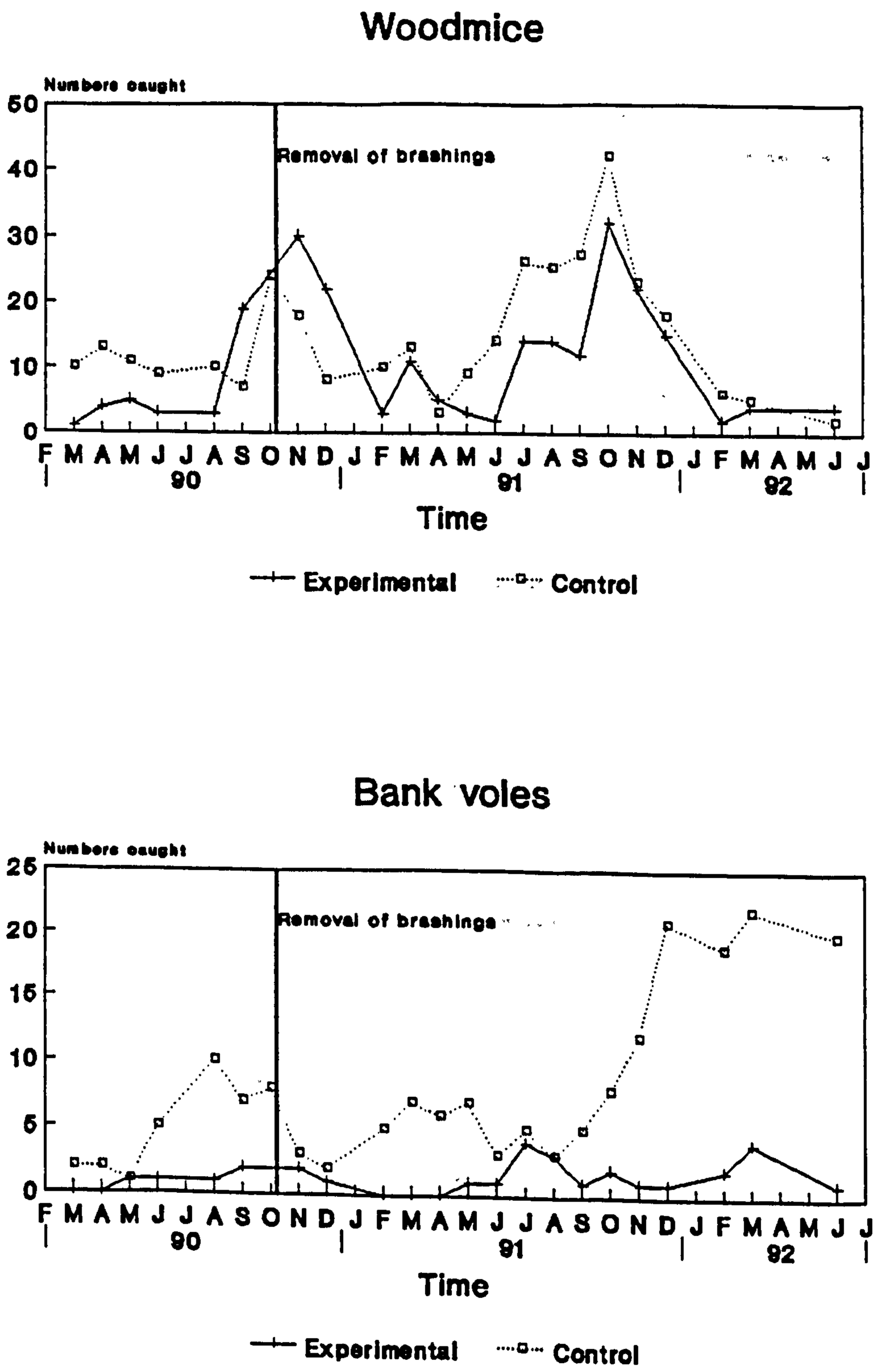
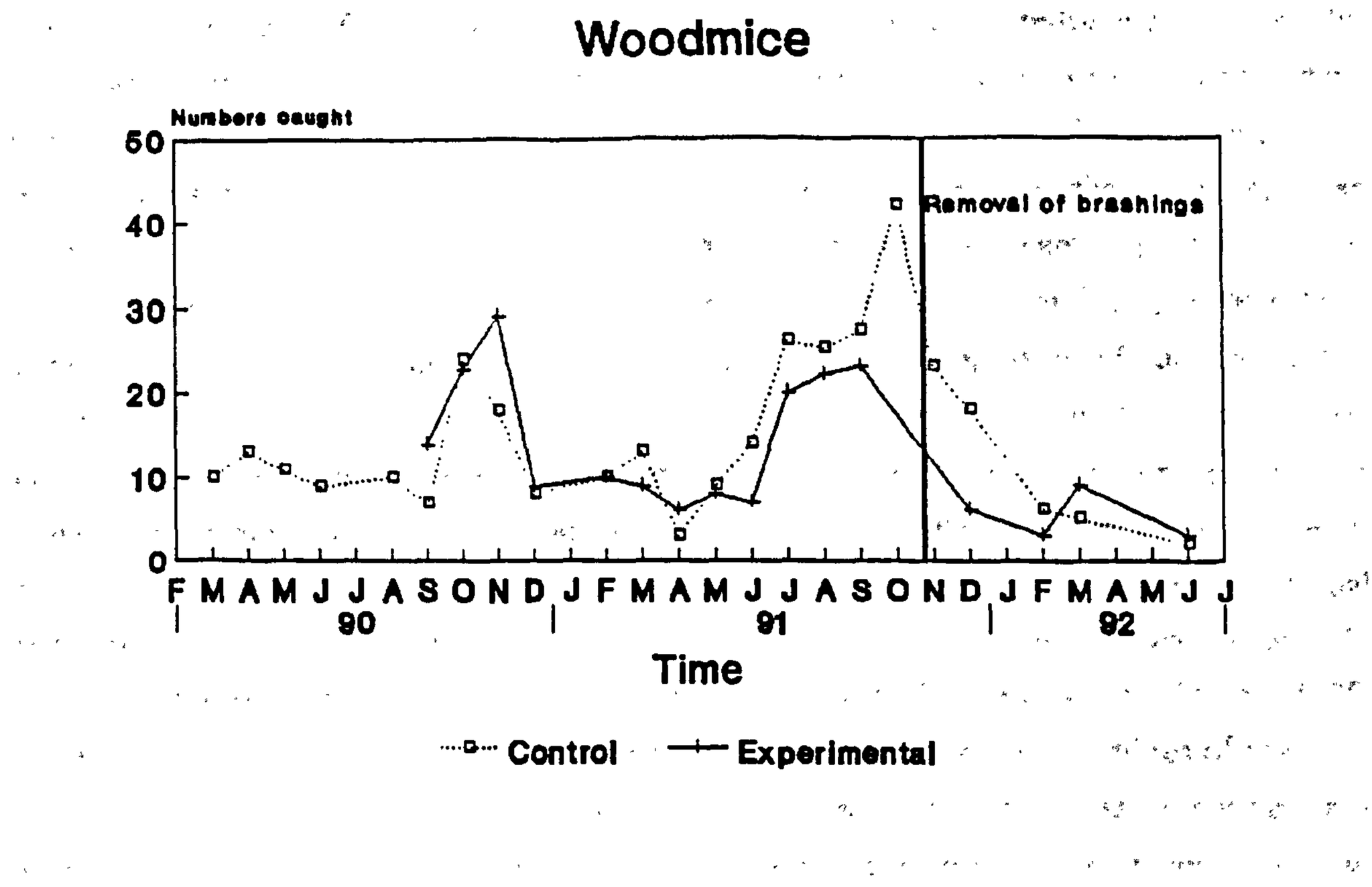
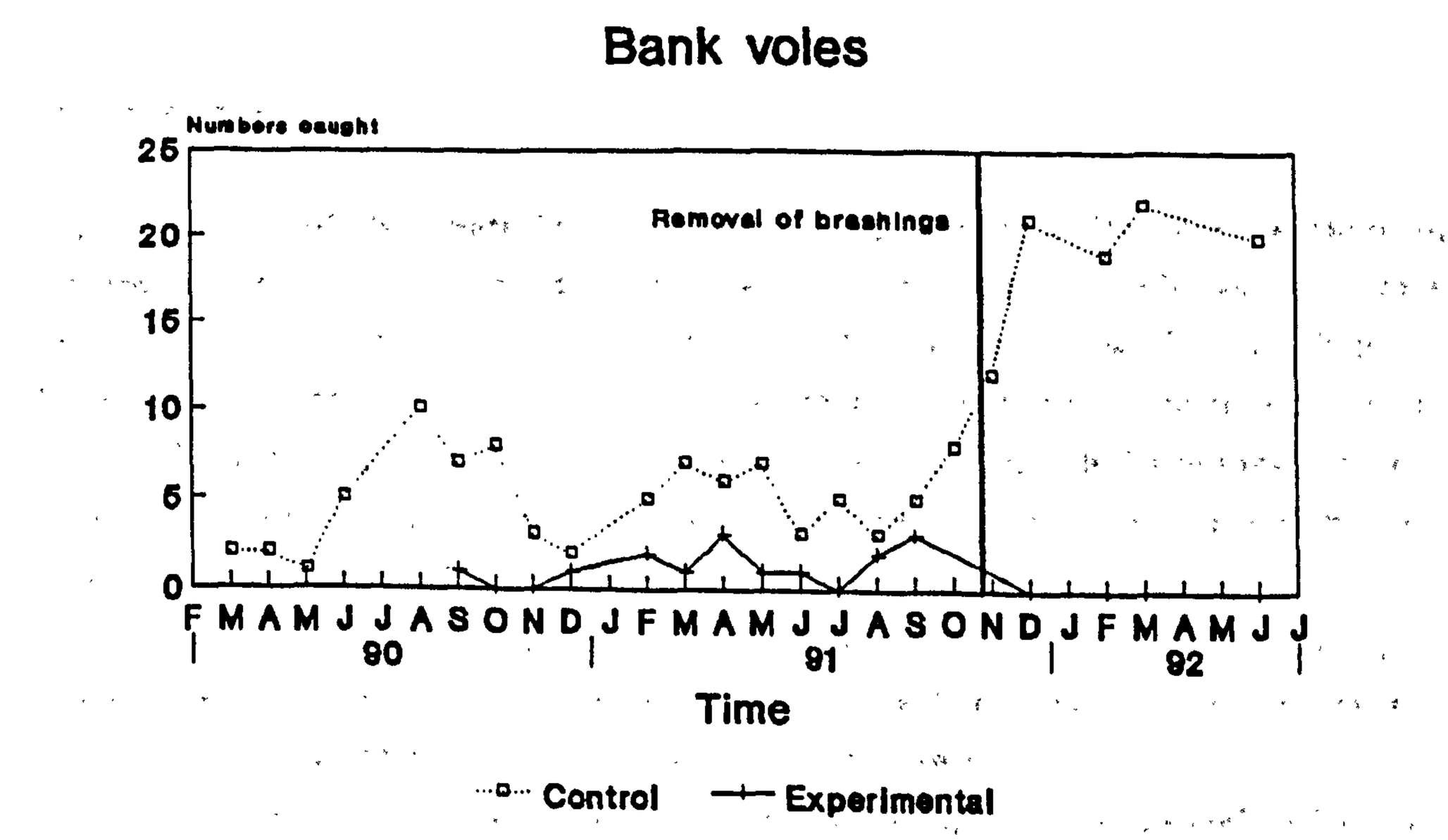


FIGURE 5.4. Effects of removal of tree brashings from clear-fellings on the abundances of rodents: second replicate. Graphs show the numbers of different individual woodmice (top) and bank voles (bottom) caught in the control grid Corner 2 and in the experimental grid Corner 3. Both sites were felled in July-August 1990, but brashings were removed from Corner 3 only, in October-November 1991 (time of removal of the brashings is indicated as a vertical line).





of woodmice was detected in Corner 3 in the first months after the brashings were removed (Figure 5.4).

5.3.3 - The effects of the removal of brashings on spatial distributions - After the brashings were removed from Corner 1, woodmice and bank voles showed contrasting patterns of distribution within this grid. The distribution of captures of woodmice did not provide a clear evidence of edge effect: the proportion of captures in the outer traps was higher than expected, but the difference was marginally non-significant (Figure 5.5; $X^2 = 3.10$, $0.05 < p < 0.10$). The captures of bank voles, on the other hand, were clearly concentrated along the edges of the grid (Figure 5.5); the proportion of captures in the outer traps was significantly higher than expected ($X^2 = 12.08$, $p < 0.01$). Further comparisons were carried out with the spatial distributions found in the same period in a clear-felling where the brashings were not removed, the control Corner 2. In Corner 2, from November 1990 to June 1992, no significant difference between expected and actual proportion of captures in the outer and inner traps was found either for woodmice (171 and 195 captures respectively; $X^2 = 0.27$; $p > 0.50$) or bank voles ($X^2 = 1.24$, $p > 0.25$; Figure 5.5). Thus, the concentration of captures of bank voles along the edges of the grids where brashings had been removed was not paralleled either by the same species in a clear-felling with brashings left in place, nor by woodmice in situations where brashings were left or were removed.

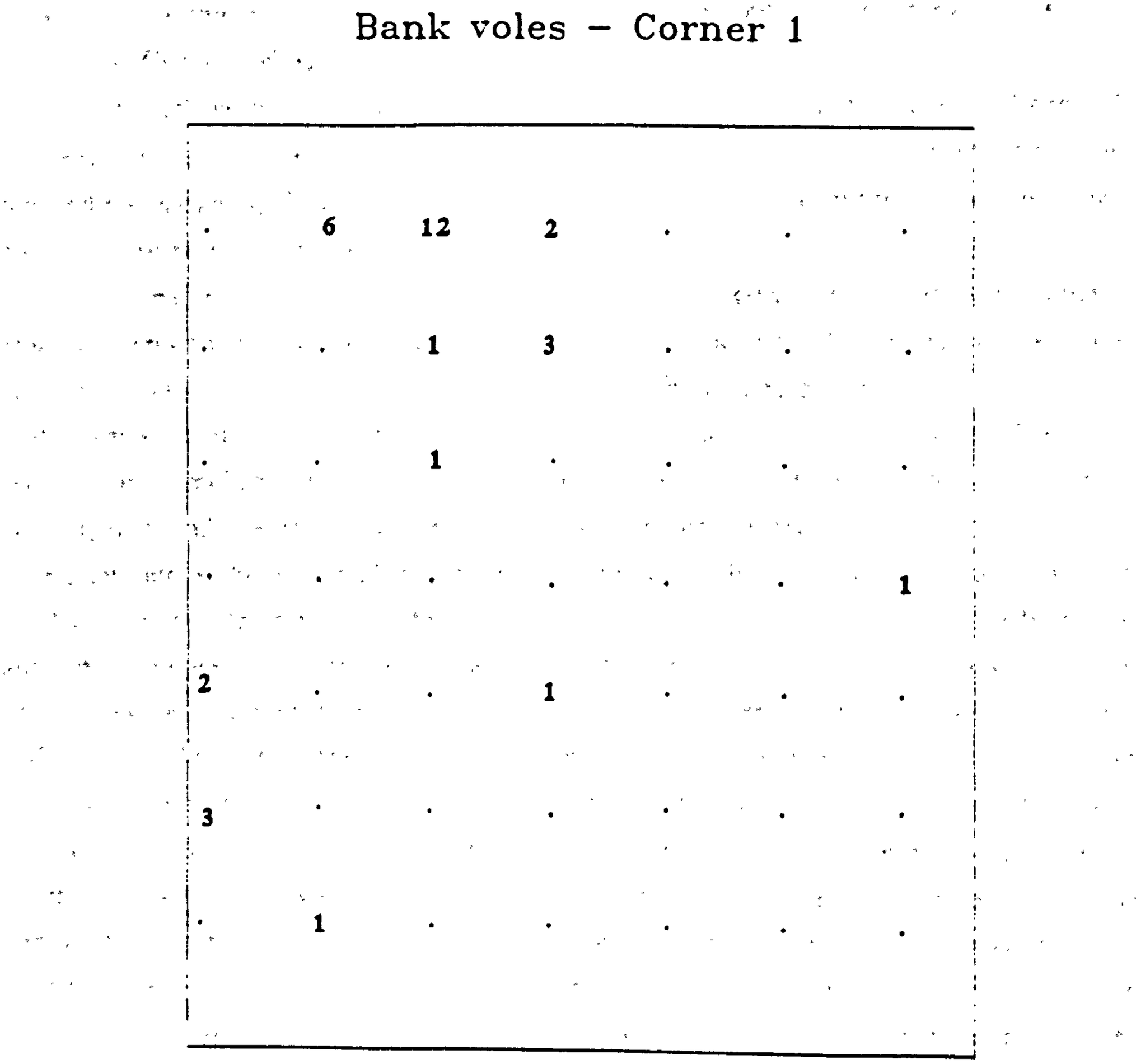
5.4 - Discussion

5.4.1 - Validity of the controls: fine scale spatial heterogeneity as a problem for experimental design - A standing Sitka spruce forest looks superficially one of the most homogeneous habitats one could find. Additionally, the study described in Chapter 3 found greatest inter-site heterogeneity amongst young plantations, not mature plantations or clear-fellings. Yet, in at least three cases I found unexpectedly large pre-experiment differences either between experimental and control areas or between areas which should have provided replicates of the same experimental treatment, as follows.

(1) Before the clear-felling of the two replicate grids Corner 1 and 2, the abundances of the two rodent species differed in the two sites, although the distance between them was only about one hundred meters (Figure 5.1).

(2) After clear-felling, the rodent communities in the three recently felled grids (Corner 1-3) and in the older clear-felled Corner South grid differed: bank voles were

FIGURE 5.5. Effects of experimental removal of brashings on the spatial distribution of rodents: number of captures (not necessarily of different individuals) in each point of a standard trapping grid. Top, bank voles in Corner 1 after the brashings had been removed (November 1990-June 1992); bottom left, woodmice in the same grid and period; bottom right, bank voles in the control grid Corner 2, where brashings were not removed, during the same period.



found only in the recent clear-fellings but not in Corner South, field voles were found (in small numbers) in Corner South only. The difference might have been explicable by the time since clear-felling: for example, if bank voles were to become gradually less abundant with time in the clear-fellings, the pattern would gradually converge to that of Corner South. That was not the case. Corner 2, where tree brashings were not removed, was supposed to be the grid most comparable to Corner South, and yet nearly two years after being felled Corner 2 showed a very high abundance of bank voles.

(3) Bank voles were nearly aways more abundant in Corner 2 than in Corner 3 between September 1990 and September 1991. The two sites were located about one hundred meters apart, they had been felled at the same time, and in the period mentioned tree brashings were still present in both.

This pattern of great heterogeneity between supposedly similar sites, which caused great problems for the interpretation of the experiments, seems to be a consequence of the fine scale spatial heterogeneity in Hamsterley as a whole. The study on successional and spatial variation in rodent communities around the whole forest (Chapter 3) had been carried out simultaneously with the population study at Corner Complex. Spatial heterogeneity of the rodent communities was greatest among young plantation sites, where any one of the three rodent species (woodmice, bank voles and field voles) could be locally dominant. In mature plantations and clear-fellings, field voles were usually absent and woodmice were usually the most abundant species. However, the absolute abundances of each species were quite variable among mature plantations or among clear-felling sites, and, in particular, bank voles were often absent from clear-fellings (see Table 3.3). At leat for young plantations, this variation in rodent communities was associated with composition and structure of vegetation, which responded to the fine scale spatial heterogeneity of soil types in the forest (Section 3.4.6). Thus, the overall pattern of spatial variation of rodent communities revealed by the simultaneous study carried out in larger spatial scale may explain the first and the third cases of inadequacy of controls described above. The second, i.e., the marked numerical dominance of bank voles in the clear-felled Corner 2 towards the end of the study, cannot be explained satisfactorily by these factors.

5.4.2 - Effects of clear-felling on the rodent populations - An unexpected result of this study was how little the sudden, drastic habitat change, produced when the trees were felled, seemed to affect the rodent populations. No obvious reduction in rodent abundance could be detected in Corner 2 in August 1990, when part of the Corner 2 grid was already felled and part not. Considering that in August only 20 traps were set in Corner 1, from which trees were still being removed, rodent densities were not obviously reduced by

felling in Corner 1 either (see Tables 5.1 and 5.2). Harrison (1990) collected additional data on short-term responses to felling. He trapped a site within Corner Complex (but not within my grids) just after it was clear-felled in June 1990. He failed to capture any animals in the first week after clear-felling (in 56 trap nights), but started to capture them again as early as the second week. As in the present study, many of the animals recaptured by him soon after clear-felling had been marked originally in the same place before the forest was cut. One may ask whether they had moved out and came back to their original home ranges after felling was over, or whether they survived felling *in situ*, but were not captured in the first week because their trappability was reduced for some reason. My results (Chapter 4) suggest that the trappability of both woodmice and bank voles in Corner Complex as a whole was lower than average around the time of felling. A clear directional pattern in the movements, first away from the areas being felled and then back after a short interval, could not be detected by Harrison (1990). Thus it is not certain whether or not the surviving animals survived *in situ*. However, what is clear is that the process of clear-felling either had no effect or only a very short-lived effect on the abundance of rodents.

After the process of removal of the trees was completed, the effects of the drastic habitat change were smaller and more gradual than expected. In the first year after felling, seasonal trends in the mature forest control grid Corner North and in the clear-felling grid Corner 2 were similar for both rodent species, abundances being only slightly higher in the control.

One year after the clear-felling had taken place marked differences began to appear. Both rodent species became significantly more abundant in the clear-felling than in the control, the difference being much more obvious in bank voles. The direction of this change in abundance was contrary to my expectation: I had predicted that woodmice would become dominant to bank voles in clear-fellings, yet the opposite gradually happened in Corner 2. Thus the outcome of the clear-felling experiment did not confirm my prediction on the relative abundances of the two species (Section 5.1.2).

As pointed out in Section 5.4.1, the high abundance of bank voles in Corner 2 during the first half of 1992 was atypical, even when compared with the other clear-fellings (with brashings left) trapped in Hamsterley Forest at a similar time, i.e. during the June 1992 census (Chapter 3). Apparently the high numbers in Corner 2 in that period were part of a long-term increase of the bank vole population in Corner Complex during more than an year (Chapter 4), plus bank voles having quite rigid habitat preferences (Chapter 6) and Corner 2 being a highly preferred grid by the end of the study. However, the question remains of why Corner 2 was preferred in relation to all other grids, including

the adjacent mature control Corner North: bank voles were usually more abundant in mature Sitka spruce forest than in clear-fellings in Hamsterley (Chapter 3). It should be noticed that Corner 2 was atypical among clear-fellings for being partly located on a *Calluna-Eriophorum* blanket bog. This substratum may well be more fertile than the soils of the remaining clear-fellings, which are mostly podzolic (Table 3.1); the soil characteristics could have allowed a good growth of ground vegetation in Corner 2 in the second year after felling, which could have favoured the bank voles. However, nearly one year after Corner 2 was felled, the ground vegetation there was no more abundant than in the remaining clear-fellings (Table 3.11). This result is not incompatible with the hypothesis above, but it does not provide support for it either. An alternative view is that the marked dominance of woodmice could be a characteristic of recent clear-fellings, but bank voles would become increasingly common a few years after clear-felling as ground cover improves. This view, however, is clearly not supported by the patterns shown by the oldest clear-fellings I studied, Corner South (present Chapter) and View (Chapter 3). All things considered, the reasons for the uniqueness of Corner 2 are not clear as in this case it is difficult to disintangle the effects of clear-felling from the effects of spatial variability.

5.4.3 - Removal of tree brashings from clear-fellings: different effects on woodmice and bank voles - As predicted, the removal of brashings from the recent clear-fellings caused little depressive effect on the abundance of woodmice. In the first replicate of the experiment (Corner 1), there was actually a short-lived "pulse" of high abundance of woodmice in the two first months after the brashings were removed. J.L. Butterfield (pers. comm.) suggested that the "pulse" could have arisen because ground invertebrates initially become easier to find on the bare ground, but soon become scarcer in the area by then devoid of most of the decaying matter which originally supported the invertebrate communities. Woodmice switch their food habits opportunistically to prey mostly on invertebrates when seed is scarce either locally or seasonally (Obrtel and Holisova, 1979, Montgomery and Montgomery, 1990, Zubaid and Gorman, 1991; see also Section 4.4.5). Additionaly, any remaining edible seeds could also be easier to find after brash removal. In California, Tevis (1956) found that mice (mostly *Peromyscus maniculatus*) were more efficient in finding seeds of Douglas-fir (*Pseudotsuga taxifolia*) in clear-fellings where the slash had been removed by burning. Whatever the reason for the "pulse", woodmice then became less abundant in Corner 1 than in the control Corner 2, but they remained present in the experimental grid in considerable abundance.

When the experiment was replicated in Corner 3 in 1991, the "pulse" of abundance did not occur. The reason for this is not clear but it may be linked to the overall wood

mouse population levels being lower in 1991 than in the previous year. Additionally, the removal of brashings took longer in 1991 than in the previous year, finishing only in November. In November 1991 the reproductive season of woodmice had nearly finished and thus the potential for population increase was reduced (Chapter 4), and by this time of the year the activity of many invertebrates in clear-fellings also decreases (J.L. Butterfield, pers. comm.). From the manipulation until the end of the study, the abundances of woodmice in Corner 3 were not significantly lower than in the control Corner 2. Considering the results of the two replicates together, it seems that the removal of the tree brashings from recent clear-fellings did not make these habitats unsuitable for *Apodemus sylvaticus*. This finding is consistent with the habitat preferences of this species described in Chapter 3, as an association between woodmice and bare soil was found in the CCA analysis (see Figure 3.8). Woodmice apparently do not depend much on cover for anti-predator defence. Being strictly nocturnal and avoiding bright moonlight (Kikkawa, 1964; Wolton, 1983), they rely on the cover of darkness, plus behavioural responses like leaping and freezing, to evade sight-oriented predators. Furthermore, woodmice can make efficient use of their complex burrow systems to escape from mustelid predators (King, 1985).

In contrast with woodmice, the abundance of bank voles was severely depressed by the removal of tree brashings. In Corner 1, bank voles were much less abundant than in the control from the time brashings were removed until the end of the study. The difference is clear, but it is necessary to keep in mind that bank voles had already been significantly more abundant in Corner 2 than in Corner 1 before the removal of the brashings. Thus, using numbers alone it is difficult to separate the effects of the experimental manipulation from the effects of spatial heterogeneity. However, the spatial distribution of captures of bank voles in Corner 1 indicates that they used the core of this grid much less often than suggested by abundance estimates alone. Most captures of bank voles in Corner 1 probably represent edge effect: individuals which inhabited chiefly areas around the grid (where brashings were left) finding peripheral traps, but seldom venturing into the core of the grid, where little cover was available.

It should be noticed that the brashings-free Corner 1 grid was quickly invaded by vegetation from spring 1991, the dominant plants by the end of the study being herbs like rosebay willowherb (*Chamaenerium angustifolium*) and sorrel (*Rumex* spp). Howéver, up to the end of the study the cover provided by these herbs was not by any means as dense as the cover provided by brashings or by cover plants prefered by bank voles elsewhere in Hamsterley, especially heather (Chapter 3).

When the experiment was replicated in Corner 3 in 1991, not a single bank vole was captured there after the brashings were removed. Although bank voles had already been less abundant in Corner 3 than in the control Corner 2 before the experiment, this result reinforces the conclusion that the removal of the brashings makes a recent clear-felling unsuitable for bank voles. Thus, most of the results of the experiment on removal of brashings, especially regarding rodent spatial distribution, upheld the prediction that the experimental manipulation would affect bank voles more than woodmice (Section 5.1.2). This finding is related to bank voles' marked preference for habitats with dense cover (Chapter 3), apparently because it provides shelter against aerial predators (Southern and Lowe, 1968, 1982, Southern, 1970). Being partly diurnal, bank voles do not make full use of the protection provided by darkness. Additionally, bank voles are not as agile as woodmice, and they tend to be flushed out of their underground burrows by mustelid predators more easily (King 1985). Thus, if no cover is available above ground to prevent bank voles being detected in the first place, they would be very vulnerable to weasels and stoats as well. Because of all these features, the anti-predator defences of bank voles depend strongly on the shelter provided by ground cover, and in recent clear-fellings only the tree brashings can provide such cover.

The findings discussed in this Section suggest that the policy of leaving tree brashings *in situ* favours diversity of rodent communities in recent clear-fellings because, although the brashings may be irrelevant for woodmice, they are a necessary factor to allow bank voles to remain in any appreciable densities in these habitats.

CHAPTER 6

RODENT POPULATIONS IN A HABITAT MOSAIC PRODUCED BY FELLING: III - DENSITY-DEPENDENCE IN HABITAT SELECTION

6.1 - Introduction

6.1.1 - Density-dependent habitat selection: pattern and processes - The idea of density-dependent habitat selection was apparently developed independently by Svärdson (1949), Morisita (1950, quoted in Rosenzweig, 1989) and Fretwell and Lucas (1970), and was later given a fuller theoretical treatment by Fretwell (1972), Rosenzweig (1981) and Morris (1987). The basic idea is that at low densities animal populations can "afford" to select just the best habitats but, at high densities of conspecifics, part of the population will be forced by competition to utilize suboptimal habitats as well. As a result, populations would be distributed more widely among habitats at high population densities, and conversely, "true" habitat preferences would be evident only at low population densities. Density-dependent habitat selection theory was originally devised for one-species situations, i.e., the models assumed interspecific interactions to be unimportant. More recent theoretical developments have extended density-dependent habitat selection theory to include the effects of interspecific interactions (e.g., Rosenzweig and Abramsky, 1986; Rosenzweig, 1989).

Since the 1980's, small mammals have been one of the taxa most often used in field studies testing density-dependent habitat selection (e.g. Rosenzweig and Abramsky, 1985, 1986; Morris, 1987; Abramsky, 1989; Montgomery, 1989c; Abramsky *et al.*; 1990, Messier *et al.*, 1990). The model has been found to apply to some species and not to others; even among congeneric species, some may be density-dependent habitat selectors and others not (Rosenzweig and Abramsky, 1985).

The studies listed above sought to detect density-dependent habitat selection by the pattern it is expected to produce, i.e., population more widely spread among different habitats at high densities than at low densities. Presumably due to the high mobility of many animals, theorists have usually assumed that this pattern is brought about by non-random movements of individuals. An "evolutionary astute" individual (Rosenzweig, 1981) would display the optimal behaviour of moving towards the habitat which best suits it at any given population density; it has been assumed that the directional population fluxes (emigration/immigration) resulting from this behaviour are the most important or

the only cause of the observed pattern (e.g. Fretwell, 1972; Abramsky and Van Dyne, 1980; Rosenzweig, 1981).

Arguably, the pattern expected from density-dependent habitat selection based on active movements among habitats could also be produced by an alternative model, arising from differences among the local (i.e. habitat level) demographies in an habitat mosaic. The reasoning is as follows. At times of low overall population density, numbers are highly variable spatially: some habitats are "poor" and other "rich" (i.e., have low and high densities respectively). When the population increases, it increases more in the "poor" habitats than in the "rich", not because of emigration/immigration but because survival and/or recruitment improve more in the poor habitats. When the population decreases, conversely, survival and/or recruitment deteriorate more sharply in the grids which originally had low densities, so restoring the original pattern. This process would be expected if (1) there is a link between population density and abundance of resources and (2) spatial distribution of resources is more aggregated when they are scarce than when they are abundant. This model would produce a pattern of animals more widely distributed among habitats at times of high population densities, i.e., the same pattern usually associated with density-dependent habitat selection. In a strict sense, the pattern should be called habitat selection only if it was generated by movements, but for convenience I follow the literature in calling the pattern "density-dependent habitat selection" throughout this Chapter, regardless of which process generates it. To my knowledge it has never been tested which one of the two alternative mechanisms described above, or which combination of the two (they are not mutually exclusive) causes the observed pattern of density-dependent habitat selection in small mammals.

6.1.2 - Assumptions and aims of the present study - The present Chapter discusses the results of a study on two rodent species - the wood mouse *Apodemus sylvaticus* and the bank vole *Clethrionomys glareolus* - within an habitat mosaic in Hamsterley Forest. As described in Chapters 4 and 5, this habitat mosaic presented spatial variation (part of the area was composed of mature Sitka spruce plantations and part of clear-fellings) and temporal variation as well (part of the felling took place during the study). However, in the present Chapter I am not concerned with the nature of the habitat variation, which was discussed in Chapter 5. Here I only make the assumption that habitat variation existed throughout the study, and I try to measure how the population densities of each rodent species affected its response to this habitat variation.

In dealing with each species separately, I make a second assumption, i.e., interspecific interactions between the two species are weak, so that habitat preferences are

more likely to be affected by the density of conspecifics than by the density of the other species. This is probably a reasonable assumption for woodmice and bank voles (Geuse and Bauchau, 1985; Gurnell, 1985; present study, Chapter 3).

The aims of the study discussed in the present Chapter were as follows.

(1) To evaluate whether habitat selection by each of the rodent species was density-dependent or not.

(2) If either species showed density-dependent habitat selection, to establish whether this pattern was caused by directional population fluxes among habitats, or by differences in local demographies, or by a combination of both.

6.2 -Methods

6.2.1 - Trapping design and trapping programme - The study area, Corner Complex, was described in Section 4.2.1. Five standard trapping grids (Corner 1, 2, 3, North and South) were trapped within this area; the position of the grids in relation to each other and to the changing habitat types was shown in Figure 4.1. The habitat changes which took place in Corner Complex during the study were discussed in Chapter 5.

Trapping was performed in Corner Complex monthly from May 1990 to June 1992. The trapping programme was described in Section 4.2.1.

6.2.2 - Estimation of demographic parameters of populations and subpopulations - Population sizes for the whole Corner Complex were estimated by the Manly-Parr method (Manly and Parr, 1968). Estimates corrected for number of grids and uncorrected estimates were both calculated. Although habitat selection is expected to be related (if at all) to population density and not to population size, population size estimates were used as an index of population density. All these aspects were discussed in Section 4.2.2.

Throughout this Chapter, "population" applies to animals living in the whole area of the Corner Complex, while "subpopulation" applies to animals living in one given grid. Estimates of size of subpopulations were given by number of different individuals captured, as dicussed in Section 5.2.2. Mortality rates for the subpopulation of a grid i (M_i) were estimated by:

$$M_i = 1 - P_{min_i}$$

Where P_{min} is minimum survival, following Chitty and Phipps (1966) and Montgomery (1980), as described in Section 4.2.2.

Per capita recruitment rates at time t were estimated as simply the number of new juvenile individuals appearing in the subpopulation between t -1 and t, divided by subpopulation size at t, just as was done for the whole population (Section 4.2.2).

Although the interval between trapping sessions was not constant, all survival and recruitment rates were transformed to 30-day rates (i.e. survival and recruitment over a period of 30 days) using the logarithmic transformations described in Section 4.2.2.

6.2.3 - Habitat selection and its relationship with population sizes - The relationship between habitat selection and population sizes was studied using two different methods.

(a) The first I derived from Ivlev's "electivity" index (Ivlev, 1961, quoted in Krebs, 1989) and hereafter is called modified Ivlev's method. Ivlev's approach was devised originally for dietary preferences, but the unmodified index has been found suitable for studies of habitat preference as well (Bowden, 1990; Grant *et al.*, 1992). In the present study I used grids as the basic habitat units; grids usually represented a single habitat type at a time, if habitat is defined either by successional stage or by experimental manipulation (Chapters 4 and 5). The value of the index for each grid is given by:

$$E_i = \frac{(R_i - M_i)}{(R_i + M_i)}$$

Where:

E_i = Ivlev's index for grid i.
R_i = percentage of individuals caught in grid i among the total caught in the m grids.
M_i = percentage of availability of grid i among the m grids.

The parameter R_i is the subpopulation size estimate for each grid; m is the number of grids that were trapped in the month under consideration; M_i is given by percentage of trapping effort spent in grid i, in relation to total trapping effort spent in the m grids. In the present study the trapping effort was the same in each grid in every month except August, 1990 (see Section 5.2.1).

The index E_i is completely based in proportions, and therefore the index itself is density-independent. It varies from -1 (no individual caught at i) to 1 (all individuals caught at i); the higher the absolute value of E_i, the stronger the preference/avoidance.

I modified Ivlev's method to evaluate the relationship between habitat selection and population density by defining a new parameter, the overall degree of habitat selection (E_o), which is given by:

$$E_o = \frac{\sum m \mid E_i \mid}{m}$$

Where $|E_i|$ is the absolute value of E_i. E_o was related to population size, N, by a simple linear regression. A significant negative slope of this regression would indicate density-dependent habitat selection. Conversely, a significant positive slope would indicate a more restricted habitat utilization at high densities, i.e., inverse density-dependence.

(b) The data were also analysed using the regression method proposed by Rosenzweig and Abramsky (1985) and used to study density-dependence in the habitat selection by gerbils in Israel's Negev desert (Rosenzweig, 1989; Abramsky *et al.*, 1990). Results obtained by this method and by the modified Ivlev's method were compared. Rosenzweig and Abramsky's method is based on their modified Simpson index, given by:

$$y' = (m.N^*.y) - m + 1 - N^*$$

Where:

y = Simpson's diversity index = $\sum_m \frac{n_i^2}{N^{*2}}$

n_i = population size at habitat i

m = number of habitats

$N^* = \sum_m n_i$ (called simply N by Rosenzweig and Abramsky; here I call it N^* to diffferentiate from the Manly-Parr population size estimate, N).

The modified Simpson's index, y', is regressed against $N^* - 1$. The technique creates a space in which habitat selectivities are given by the slopes of either one single straight line, or several straight lines which intersect at the origin. There are three kinds of possible results, as follows. (1) If there is no habitat selection at all (i.e. the species is distributed at random), y' values will be scattered around a line parallel to the x axis, i.e. with slope zero. (2) If there is density-independent habitat selection, the plot will again produce a single straight-line scatter diagram, but this time with a constant, positive slope. (3) If there is density-dependent habitat selection, the scatter diagram will form a complex function comprising a sequence of three straight lines connected to each other. The points

follow a steep positive slope from the origin until some threshold population size is reached. The slope then changes to negative as habitat selection decreases as a function of the increased population size. A second inflexion then occurs leading to a third straight line, which may reach a second, less steep positive slope reflecting the disparate ability of the habitats to support the species. This expected curve is shown in Rosenzweig and Abramsky (1985) and Rosenzweig (1989) and also in the present Chapter, where it is compared with my results (see Figure 6.3, bottom).

Rosenzweig and Abramsky's method assumes that proportions of trapping effort spent in each grid each month are constant. Thus, estimates for August 1990, when trapping effort was reduced in grids Corner 1 and Corner 2 (Section 5.2.1), could not be calculated using this method.

6.2.4 - Inter-grid movements and the estimation of emigration and immigration rates - Movements between grids were detected by recaptures, in any grid, of individuals previously captured elsewhere. For rodent species actually showing a pattern of density-dependent habitat selection, such inter-grid movements were used to test whether there was a relationship between the direction of movements and population densities in each grid, as expected if the pattern was caused mostly by non-random movements. Frequency of movements was related to subpopulation sizes in the grids of origin and destination of each movement, by using Ivlev's E_i indices to classify grids as holding either high numbers (Hn) or low numbers (Ln) at time t, if they had respectively positive or negative values of E_i at time t. Movements involving grids with average numbers (Ivlev = 0) were discarded from the analysis. For each season, the frequency of each possible type of movement (e.g from a Hn grid to a Ln grid) was calculated by dividing number of recorded movements by number of individuals available to move. In the example given, this was done by dividing the number of Hn to Ln movements by the total number of different individuals present in all Hn grids during the season under consideration.

Emigration and immigration rates for grid i at month t were calculated as follows: frequency of inter-grid movements from and towards i respectivelly, in the period from t-1 to t, divided by population size in grid i at t-1. Values were converted to 30-day rates using the logarithmic transformation described in Section 4.2.2.

6.2.5 - Relationship between changes in spatial distribution and the demographic parameters of the subpopulations - The processes accounting for the changes in the spatial distribution within the population were studied by relating variation in the size of

subpopulations with estimates of recruitment, mortality, immigration and emigration for each subpopulation. Variation in the size of subpopulations was given by:

$$dN_{i,t} = \frac{(N_{i,t} - N_{i,t-1})}{N_{i,t-1}}$$

The resulting values were converted to 30-day rates using the logarithmic transformations described in Section 4.2.2, and then related to the remaining demographic parameters for subpopulations using the following multiple regression model:

$$dN_{i,t} = a.R_{i,t} - b.M_{i,t} + c.I_{i,t} - d.E_{i,t} + e$$

Where:

$R_{i,t}$, $M_{i,t}$, $I_{i,t}$, $E_{i,t}$ = recruitment, mortality, immigration and emigration rates respectively, for grid i at time t (see Sections 6.2.2 and 6.2.4).

a,b,c,d,e = fitted regression constants.

The relative importance of the four demographic factors can be assessed by comparing the partial regression coefficients of each factor. As the goal was to understand the processes which accounted for variation in the spatial distribution within the whole Corner Complex, data were pooled for all grids. However, the regression analysis was performed separately for cases in which subpopulations were increasing ($dN_t > 0$) and decreasing ($dN_t < 0$), because the relative importance of the demographic factors is likely to be different in the two situations. Cases in which $dN_t = 0$ (i.e. absence of variation in the dependent variable) were discarded from the analysis.

6.3 - Results

6.3.1 - The relationship between habitat selection and population sizes - The number of woodmice and bank voles actually caught in each grid and month is shown in Tables 5.1 and 5.2 respectively (Chapter 5). From those data Ivlev indices for preference/avoidance of individual grids (E_i) plus overall degree of habitat selection (E_o) were calculated for rodent species (Tables 6.1 and 6.2). The E_i indices showed that no grid was consistently preferred or avoided by woodmice throughout the study, although in

TABLE 6.1 - Monthly variations of Ivlev's habitat selection indices for individual trapping grids (E_i) plus the overall degree of habitat selection in the whole study area (E_o, last column) for *Apodemus sylvaticus*.

Time	Co1(M-F) E_i	Co2(M-F) E_i	Co3(F) E_i	CoS(F) E_i	CoN(M) E_i	Overall (Eo)
1990						
May	**-0.25**	**0.14**	-	-0.02	**0.04**	0.113
Jun	**-0.40**	**0.13**	-	0.13	**0.00**	0.165
Jul	Felling	Felling	-	-	-	-
Aug	0.05*	0.24*	-	-0.38	**-0.05**	0.180
Sep	0.29	-0.20	0.15	-0.55	**-0.07**	0.252
Oct	BrashRem	0.02	0.00	0.00	**-0.02**	0.010
Nov	*0.19*	-0.07	0.17	-0.23	**-0.23**	0.178
1991						
Mar	*0.01*	0.09	-0.09	-0.57	**0.25**	0.202
Apr	*-0.02*	-0.27	0.07	0.07	**0.07**	0.100
May	*-0.42*	0.10	0.04	-0.10	**0.20**	0.172
Jun	*-0.71*	0.08	-0.26	-0.33	**0.44**	0.364
Jul	*-0.22*	0.09	-0.04	-0.15	**0.20**	0.140
Aug	*-0.23*	0.06	0.00	-0.10	**0.18**	0.114
Sep	*-0.33*	0.06	-0.02	0.11	**0.08**	0.120
Oct	*-0.06*	0.07	BrashRem	0.10	**-0.15**	0.095
Nov	*-0.02*	0.00	BrashRem	0.12	**-0.12**	0.065
Dec	*0.01*	0.10	*-0.42*	0.22	**-0.10**	0.170
1992						
Feb	*-0.31*	0.22	*-0.12*	0.14	**-0.12**	0.182
Mar	*-0.13*	-0.02	*0.27*	-0.02	**-0.27**	0.142
Jun	*0.21*	-0.13	*0.07*	-1.00	**0.21**	0.324

Note. Successional stages of the grids are: M, mature; F, clear-felling. Values for mature grids are shown in **bold**; clear-fellings in standard; experimental (brash removed) plots *italics*. E_i's are based on data from Table 5.1. For each month, E_o is given by the average of the absolute values of E_i's. Asterisks (*) indicates cases when incomplete grids were trapped during felling.

TABLE 6.2 - Monthly variations of Ivlev's habitat selection indices for individual trapping grids (E_i) plus the overall degree of habitat selection in the whole study area (E_o, last column) for *Clethrionomys glareolus*. All symbols as in Table 6.1.

Time	Co1(M-F) E_i	Co2(M-F) E_i	Co3(F) E_i	CoS(F) E_i	CoN(M) E_i	Overall (Eo)
1990						
May	**0.14**	**0.14**	-	-1.00	**0.14**	0.355
Jun	**-0.38**	**0.38**	-	-1.00	**0.14**	0.475
Jul	Felling	Felling	-	-	-	-
Aug	-0.46*	0.24*	-	-1.00	**0.25**	0.488
Sep	-0.20	0.30	-0.58	-1.00	**0.14**	0.444
Oct	BrashRem	0.25	-1.00	-1.00	**0.36**	0.653
Nov	*0.00*	0.20	-1.00	-1.00	**0.43**	0.526
1991						
Mar	*-1.00*	0.32	-0.56	-1.00	**0.47**	0.670
Apr	*-0.41*	0.43	0.11	-1.00	**-0.09**	0.408
May	*-0.52*	0.37	-0.52	-1.00	**0.37**	0.556
Jun	*-0.47*	0.03	-0.47	-1.00	**0.53**	0.500
Jul	*0.05*	0.16	-1.00	-1.00	**0.33**	0.508
Aug	*-0.23*	-0.23	-0.41	-1.00	**0.54**	0.482
Sep	*-0.62*	0.09	-0.17	-1.00	**0.48**	0.472
Oct	*-0.47*	0.19	BrashRem	-1.00	**0.37**	0.508
Nov	*-0.68*	0.39	BrashRem	-0.68	**0.14**	0.473
Dec	*-0.68*	0.60	*-1.00*	-0.68	**-0.27**	0.646
1992						
Feb	*-0.43*	0.58	*-1.00*	-0.67	**-0.25**	0.586
Mar	*-0.18*	0.58	*-1.00*	-0.71	**-0.49**	0.592
Jun	*-0.71*	0.54	*-1.00*	-0.71	**0.14**	0.620

Note: Based on data from Table 5.2.

most cases each grid remained in either category for several consecutive months (Table 6.1). For bank voles preferences/avoidances of individual grids, as shown by E_i, were stronger and more consistent than for woodmice. Corner North and Corner 2 were consistently prefered, and Corner 1 and Corner South were consistently avoided (Table 6.2). Indeed, no bank vole was captured in Corner South before November 1991. Habitat selection by bank voles was stronger than by woodmice, as E_0's were significantly higher for the former species than for the later (t test, 18 d.f., $t = -14.088$, $p < 0.0001$).

For both species, overall degree of habitat selection (E_0) was regressed against population sizes using both corrected and uncorrected population size estimates, and results using both types of estimates were compared. In both cases, regressions were significant or not regardless of which set of population size estimates was used. All the results that follow are based on the original (uncorrected) estimates. The corresponding results based on corrected estimates are presented in Appendix 3.

For woodmice, variation in E_0 was inversely related to variation in population size (Figure 6.1). The linear regression of E_0 against population size was significant (Figure 6.2) and its slope was negative and significantly different from zero ($t = -2.273$, $p < 0.05$). Variation in population size explained nearly one quarter of the variance in the degree of habitat selectivity ($r^2 = 0.233$). These results indicate that there was density-dependent habitat selection in woodmice within the Corner Complex.

No conclusive result could be obtained by applying Rosenzweig and Abramsky's method to woodmice (Table 6.3). The linear regression of the modified Simpson's indices y' against population sizes (N* - 1) was not significant (Figure 6.3, top). Thus, there was no evidence for either the hypothesis of no habitat selection at all (which would correspond to a constant slope of zero) or the hypothesis of density-independent habitat selection (constant, positive slope). However, the scatter of the points was also not obviously correspondent to the shape expected for density-dependent habitat selection (Figure 6.3, bottom). Comparing the two halves of Figure 6.3, it can be seen that my results had a superficial similarity with the expected pattern, but there were also three differences. First, there was no straight line with steep positive slope starting from the origin. Second, there was little evidence of a second straight line showing the gradual decline of the y's values after they reach the maximum, which would reflect the density-dependence. The maximum y' looks more like an isolated point than like a threshold. Third, there was no evidence of a second positive slope at all. In summary, for woodmice Rosenzweig and Abramsky's method did not allow me to distinguish conclusively between the three competing hypothesis: no habitat selection, density-independent habitat selection, and density-dependent habitat selection.

FIGURE 6.1. Variation of wood mouse population sizes (estimated by the Manly-Parr method) and degree of habitat selection (E_0) estimated by the modified Ivlev's method.

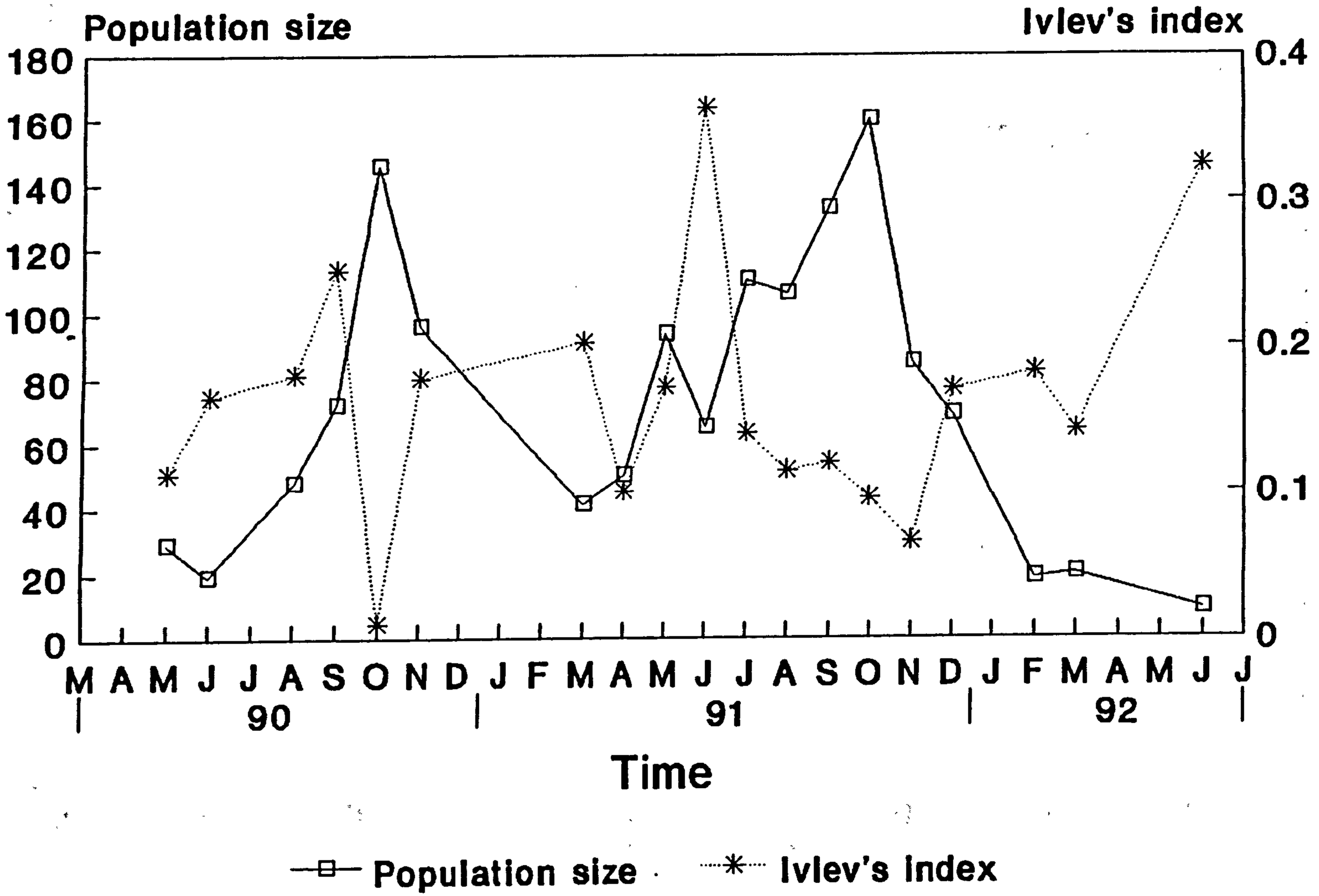


FIGURE 6.2. Scatterplot relating the variation in wood mouse population sizes estimated by the Manly-Parr method (x-axis) against degree of habitat selection (E_o) estimated by the modified Ivlev's index (y-axis). The equation which best fits the data and the corresponding regression line are shown.

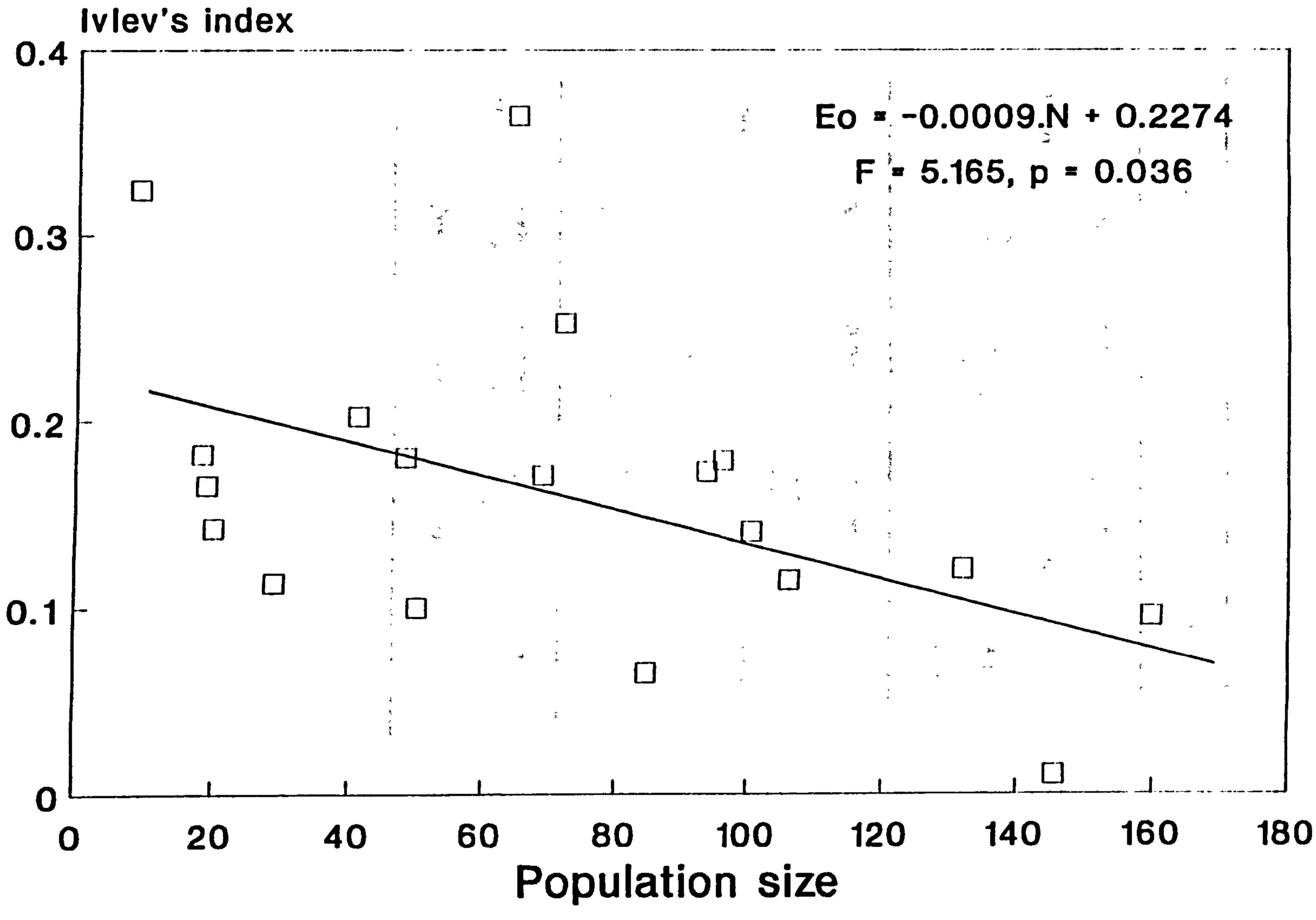
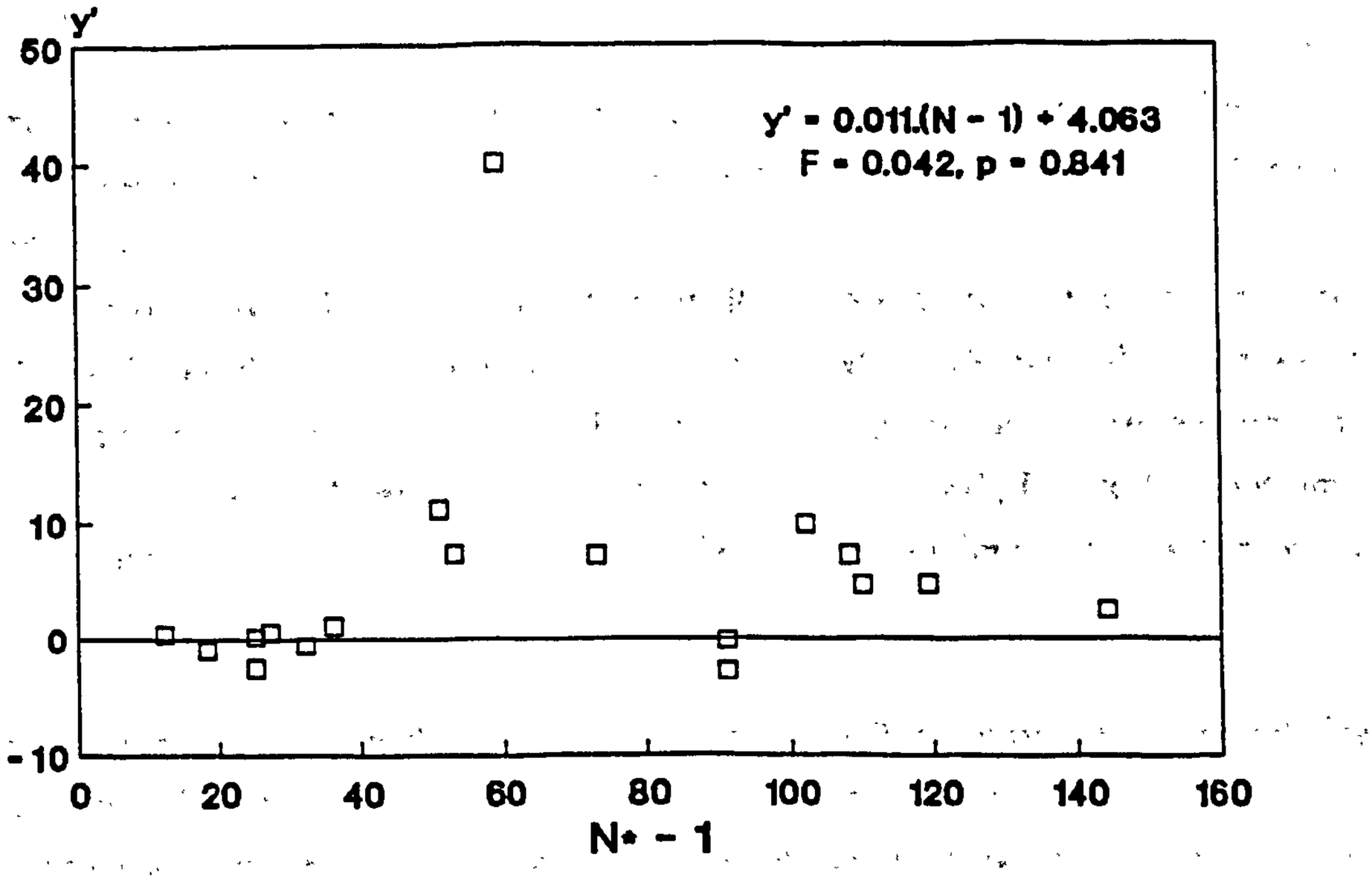
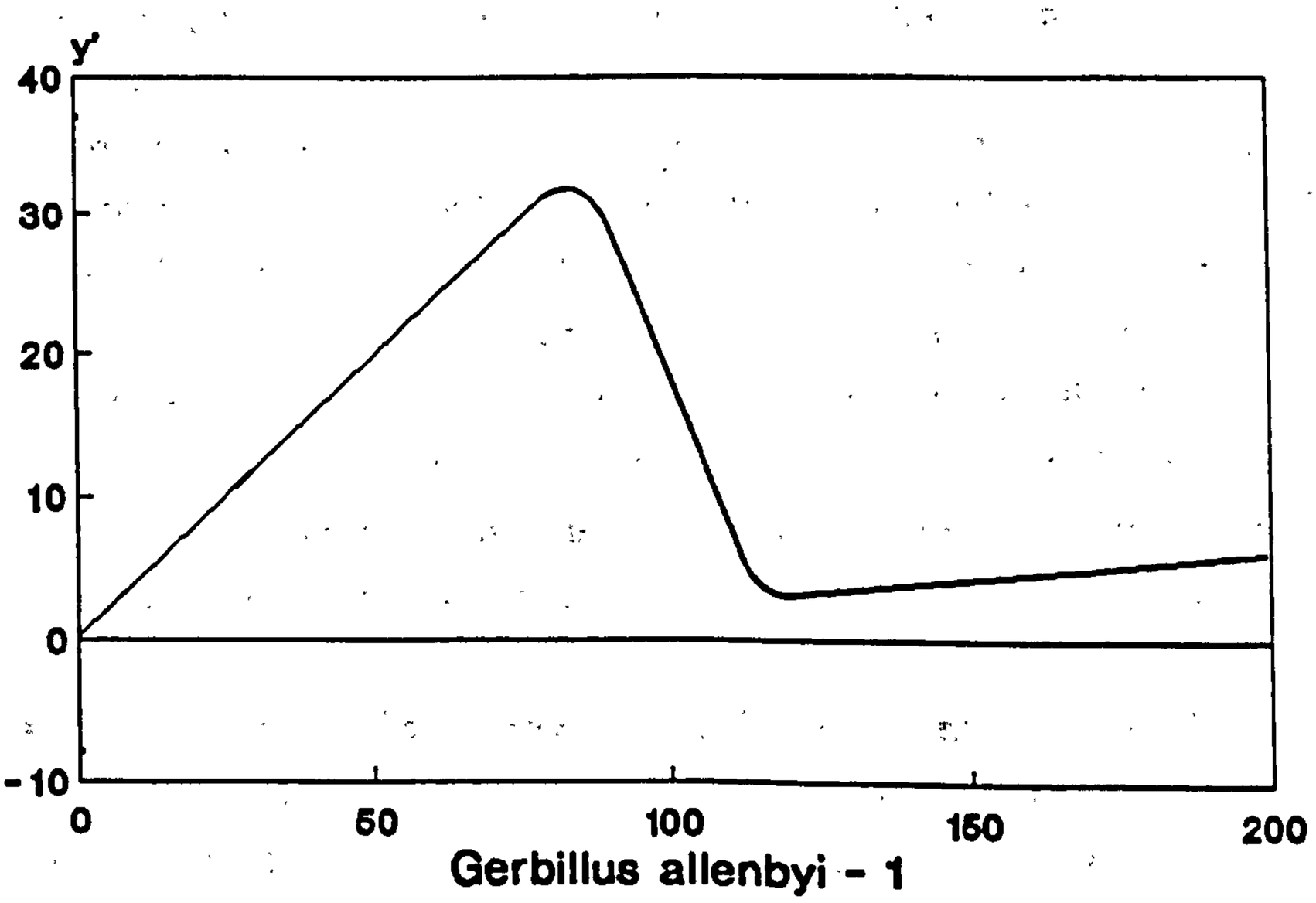


TABLE 6.3. Values for Rosenzweig and Abramsky's regression method applied to habitat selection in woodmice. y are values for the Simpson index based on data from Table 5.1, and y' are the corresponding values of the modified Simpson index (see text). N* represents the sum of the numbers of individuals in all grids.

Time		y	y'	N* - 1
1990	May	0.2672	-0.7296	32
	Jun	0.2806	0.4276	27
	Jul		Not calculable	
	Aug		Not calculable	
	Sep	0.2574	10.9240	51
	Oct	0.2502	-2.9624	91
	Nov	0.2265	9.6475	102
1991	Mar	0.2414	7.1780	53
	Apr	0.2101	-0.2687	25
	May	0.2272	1.0320	36
	Jun	0.3461	39.8300	59
	Jul	0.2203	7.0635	108
	Aug	0.2153	4.4915	110
	Sep	0.2143	4.5800	119
	Oct	0.2594	2.4520	144
	Nov	0.2573	-0.3136	91
	Dec	0.2297	6.9890	73
1992	Feb	0.2299	-1.1595	18
	Mar	0.2308	0.0004	25
	Jun	0.2663	0.3095	13

FIGURE 6.3. Top: Scatterplot of the variation in wood mouse population sizes against breadth of habitat utilization measured by modified Simpson's indices; both parameters estimated according to Rosenzweig and Abramsky's (1985) method. Bottom: an example of the typical pattern for a density-dependent habitat selector; redrawn from Rosenzweig, 1989.





For bank voles the modified Ivlev's index E_o seemed to actually increase rather than decrease with population size (Figure 6.4). This would produce a regression with a positive rather than negative slope; however, the regression was not significant ($F = 3.321$, $p = 0.086$; Figure 6.5, top). Furthermore, omitting the May 1991 point (which is based on data from 3 individuals only) the fit of the regression was very poor ($F = 0.739$, $p = 0.408$). Thus, in contrast with the findings for woodmice, the use of Ivlev's modified index did not provide evidence that habitat selection in bank voles within Corner Complex was density-dependent.

Analysis of bank vole habitat selection by Rosenzweig and Abramsky's method (Table 6.4) confirmed the patterns revealed by the modified Ivlev's method. There was a highly significant regression between y' and (N* - 1); the slope of this regression was positive and significantly different from zero ($t = 6.790$, $p < 0.001$; Figure 6.5, bottom). Thus both methods provided evidence of strong density-independent habitat selection by bank voles within the Corner Complex.

6.3.2 - Frequency of inter-grid movements - Out of 1,931 recaptures of woodmice within the Corner Complex, 294 revealed inter-grid movements. For bank voles, only 24 inter-grid movements were detected, out of 430 recaptures of individuals of this species. Thus, woodmice moved between grids significantly more often than bank voles ($X^2 = 27.243$, $p < 0.0001$).

The numbers of inter-grid movements recorded for each species in each month, and with grid of origin and of destination, are shown in Tables 6.5 and 6.6. The first clear pattern is that movements between Corner North and Corner 2 were more frequent than between any other pair of grids. These two grids are among the closest to each other, although distances between Corner 1 and 3 and between Corner 1 and Corner South were similar (Figure 4.1). Almost all inter-grid movements of bank voles were restricted to the Corner North-Corner 2 pair, these two grids being those where bank vole population sizes were highest; however, no significant difference was found between the directions moved within this pair (Table 6.6). As compared to bank voles, woodmice showed many more movements between pairs of grids other than Corner North-Corner 2 (Table 6.5). However, no significant difference was found in the frequency of movements in the two directions within any pair.

As density-dependent habitat selection could be demonstrated only for woodmice, analysis of the directionality of the movements and of their importance for spatial distribution was carried out for this species only. Frequencies of movements from low numbers (Ln) to high numbers (Hn) grids and vice-versa were compared by chi-square

FIGURE 6.4. Variation of bank vole population sizes (estimated by the Manly-Parr method) and degree of habitat selection (E_0) estimated by the modified Ivlev's method.

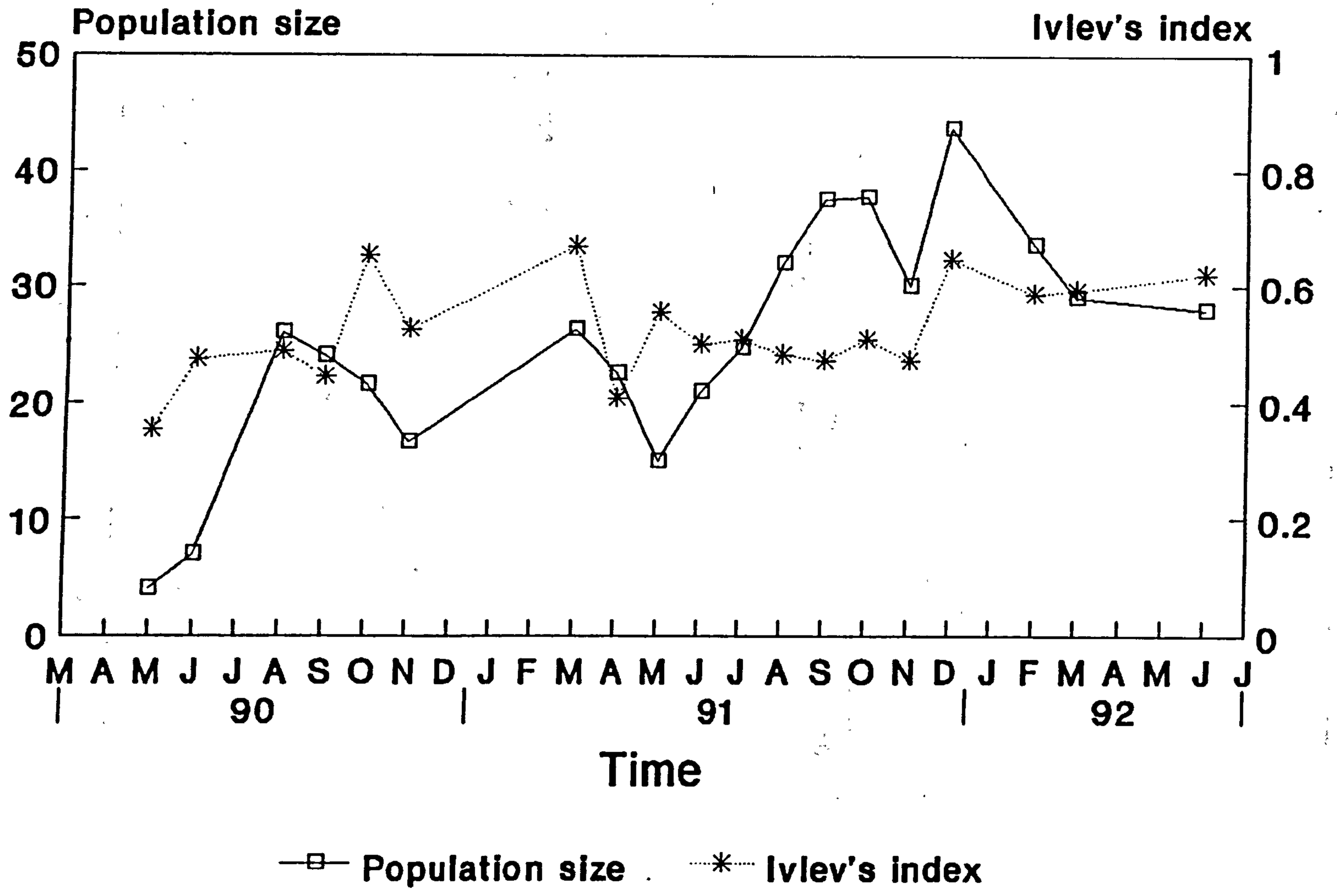
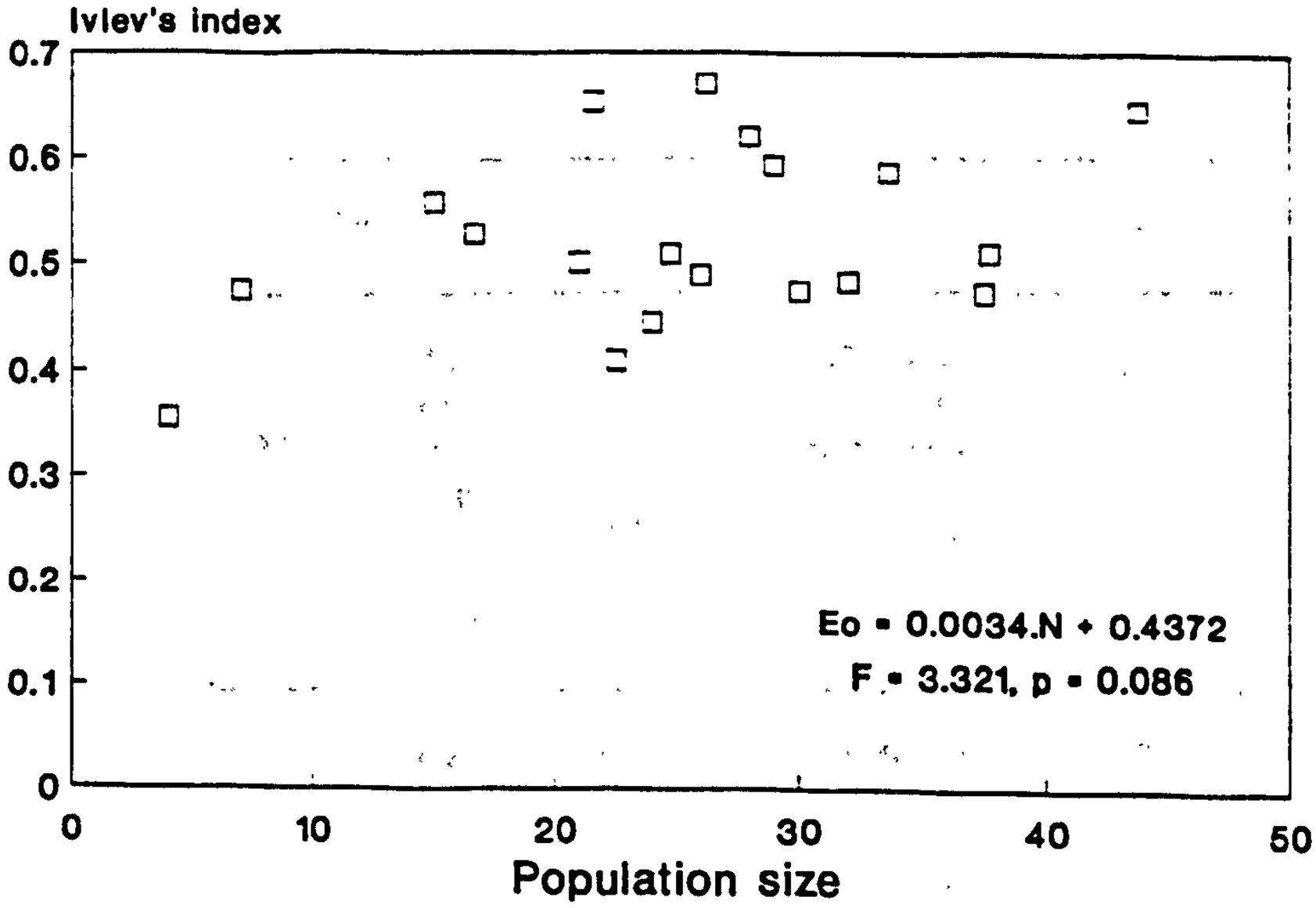


FIGURE 6.5. Scatterplots showing the relationship between population sizes and habitat selection in bank voles as shown by the modified Ivlev's method (top) and by the Rosenzweig and Abramsky's method (bottom). The regression line which best fits the data using the latter method is shown. Symbols as in Figures 6.2 and 6.3 respectivelly.



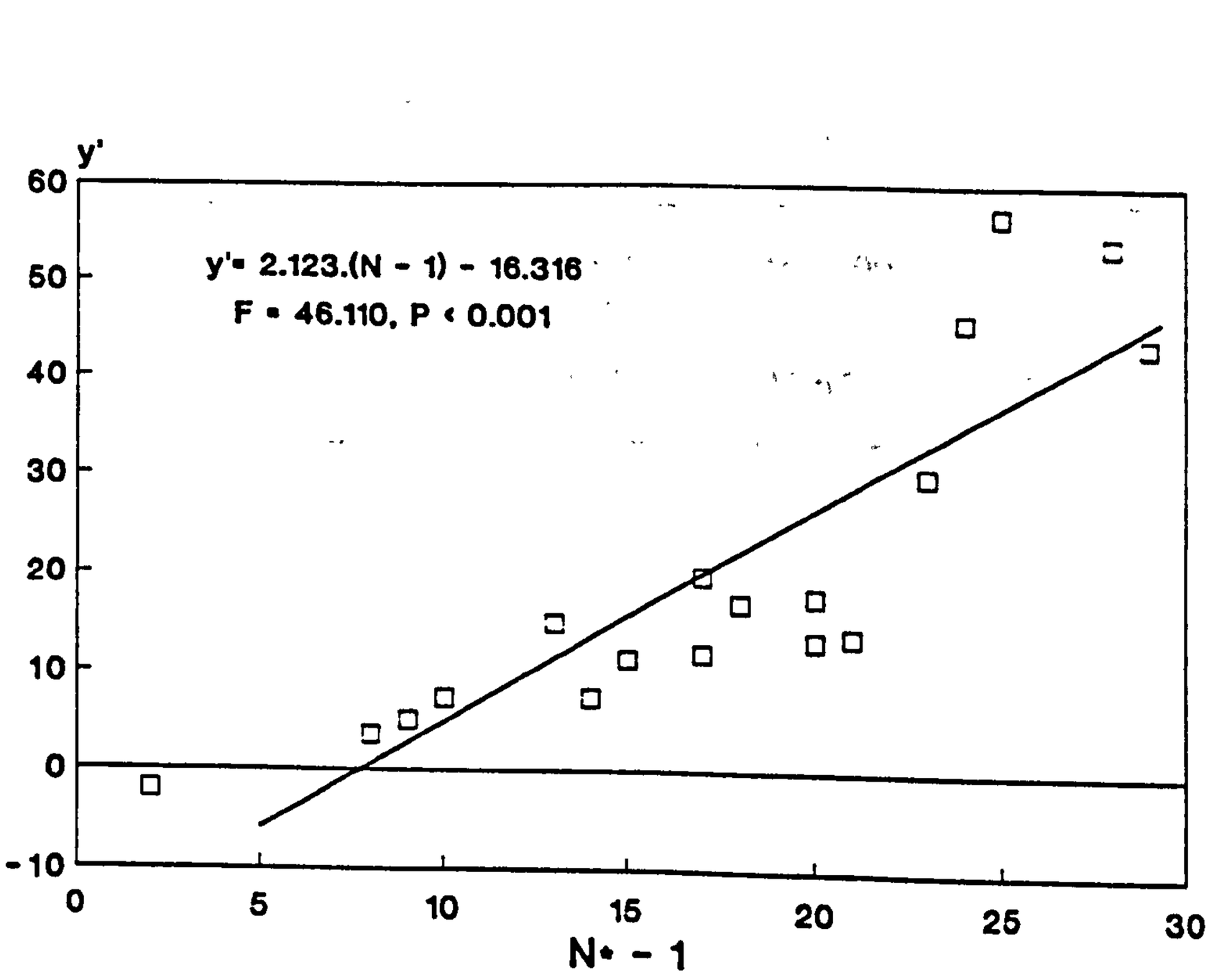


TABLE 6.4. Values for Rosenzweig and Abramsky's regression method applied to habitat selection in bank voles. Based on data from Table 5.2; all symbols as in Table 6.3.

Time		y	y'	N* - 1
1990	May	0.3333	-2.0004	2
	Jun	0.4321	3.5556	8
	Jul		Not calculable	
	Aug		Not calculable	
	Sep	0.3511	7.3325	14
	Oct	0.5125	16.9500	18
	Nov	0.3800	5.0000	9
1991	Mar	0.4630	19.6700	17
	Apr	0.4050	7.2750	10
	May	0.3906	11.2480	15
	Jun	0.4694	14.8580	13
	Jul	0.3765	11.8850	17
	Aug	0.4826	29.9120	23
	Sep	0.4059	17.6195	20
	Oct	0.4380	13.5440	21
	Nov	0.4422	13.1448	20
	Dec	0.6686	56.9180	25
1992	Feb	0.6000	46.0000	24
	Mar	0.6005	54.0725	28
	Jun	0.5178	43.6700	29

TABLE 6.5. Inter-grid movements of *Apodemus sylvaticus* within the Corner Complex.

Month of arrival in new grid	Pairs of grids									
	N-1	N-2	N-3	N-S	1-2	1-3	1-S	2-3	2-S	3-S
1990										
Mar	-	-	-	-	1/0	-	-	-	-	-
Apr	-	-	-	-	0/1	-	-	-	-	-
May		2/0	-		0/1	-		-		-
Jun			-		1/1	-		-		-
Jul		0/2			-					
Aug		5/0			0/1					
Sep	0/1	0/1					0/1			0/2
Oct		1/0								1/6
Nov		1/1				0/5	4/1	1/2	0/1	4/1
Dec				-		2/1	0/3			
1991										
Feb				-		0/2		2/2		
Mar		0/8				3/1	1/0	0/1		
Apr		1/1				2/3				3/0
May		2/3				1/0		0/1		0/1
Jun		2/5				1/1		0/3		
Jul		7/11			2/0	1/3		2/1		
Aug	0/1	8/8			0/1	1/1	1/0	3/1		2/2
Sep		5/0		1/1		1/1	1/2	2/3		0/1
Oct	0/1	8/14			0/1	0/3	9/0	0/1	1/0	2/0
Nov		8/11		1/0		0/1	10/1			
Dec		8/6					4/9			
1992										
Feb		2/2				1/0	0/1		0/1	0/1
Mar		3/2	0/1				1/1	1/0		1/0
Totals	0/3	63/75	0/1	2/1	4/6	14/22	31/19	11/15	1/2	13/14
X^2 (p)	NC	0.877 (>.25)	NC	NC	0.100 (>.75)	1.361 (>.10)	2.420 (>.10)	0.183 (>.50)	NC	0.000 (>.90)

Note. The first number refers to movements in the direction in which the grids are quoted in the top line of the table, and the second number to movements in the opposite direction. Blank spaces indicate cases where no movement was detected; traces (-) indicate cases where no movement could be detected because either grid of the pair was not being trapped at the time. Last line: results of the chi-square test comparing the frequency of movements in each direction within each pair of grids; all chi-square tests with Yates' correction for continuity; NC = not calculable.

TABLE 6.6. Inter-grid movements of *Clethrionomys glareolus* within the Corner complex. All symbols as in Table 6.5.

Month of arrival in new grid	Pairs of grids									
	N-1	N-2	N-3	N-S	1-2	1-3	1-S	2-3	2-S	3-S
1990										
Mar	-	-	-	-		-	-	-	-	-
Apr	-	-	-	-		-	-	-	-	-
May			-			-		-		-
Jun			-			-		-		-
Jul					-					
Aug										
Sep										
Oct		1/0	0/1							
Nov		0/1								
Dec				-						
1991										
Feb				-						
Mar		0/2								
Apr		2/1							1/0	
May					1/0					
Jun		0/1								
Jul										
Aug										
Sep		2/0								
Oct		1/0								
Nov		1/1							0/1	
Dec		3/1								
1992										
Feb		1/1								
Mar		1/0								
Total	0/0	12/8	0/1	0/0	1/0	0/0	0/0	1/1	0/0	0/0
X^2 (p)	NC	0.450 (>.50)	NC	NC	NC	NC	NC	NC	NC	NC

tests (Table 6.7) and shown as a histogram in Figure 6.6. In 1990, frequencies of movements in the two directions were similar in spring, but movements from Ln to Hn grids were significantly more common than movements in the opposite direction during the summer of 1990 ($X^2 = 8.431$, $p < 0.01$), a time of low overall population size. During autumn 1990 and winter 1991, when overall population sizes were high for most of the time, movements from Hn to Ln grids seemed to be more common than vice-versa, but the difference was not significant. In spring 1991, with low overall population sizes, movements from Ln to Hn grids were again significantly more common than movements in the reverse direction ($X^2 = 5.222$, $p < 0.05$). This same trend was apparent through the rest of 1991 (with high population sizes) but especially marked towards the end of the study in spring 1992 (with very low population sizes); however, in neither case were there significant differences.

6.3.3 - Demographic parameters of subpopulations and their relationship with variations in numbers at grid level - Thirty-day per capita rates of variation in the number of woodmice caught at each grid in each month ($dN_{i,t}$) are shown in Table 6.8. Corresponding mortality ($M_{i,t}$) and recruitment ($R_{i,t}$) rates are shown in Table 6.9, and emigration ($E_{i,t}$) and immigration ($I_{i,t}$) rates in Table 6.10.

Distributions of the demographic rates were not normal and a $x' = \log (x + 1)$ transformation was applied before regression analysis. The multivariate regression of log ($dN_{i,t}$) against the logarithm of the four demographic rates produced highly significant equations both at times of population increase ($dN_{i,t} > 0$) and at times of population decrease ($dN_{i,t} < 0$). During population increase, recruitment and immigration showed significant positive partial regression coefficients (Table 6.11). Mortality had a significant negative coefficient and the partial coefficient for emigration was not significant. In order of proportion of variance explained (measured by r^2) recruitment was by far the most important variable, followed by immigration and mortality in this order. During population decrease, mortality and emigration had significant negative partial regression coefficients (Table 6.11). Recruitment had a significant positive coefficient and the partial coefficient for immigration was not significant. Mortality explained most variance, followed by recruitment and emigration in this order.

TABLE 6.7. Numbers of movements of *Apodemus sylvaticus* as a proportion of number of individuals available to move. Movements classified according to the Ivlev's indices (E_i) of the grids involved (prefered (+) or avoided (-)) and seasons.

Season (n)	Type of movement				X^2
	- to -	+ to +	- to +	+ to -	
1990					
Spring (79)	0/24	2/55	1/24	2/55	0.277 NS
Summer (110)	0/37	2/73	8/37	2/73	8.431 **
Autumn (247)	1/108	11/139	4/108	12/139	1.692 NS
1991					
Winter (77)	0/35	8/42	2/35	4/42	0.038 NS
Spring (177)	2/57	16/120	7/57	3/120	5.222 *
Summer (400)	8/143	40/257	13/143	13/257	1.840 NS
Autumn (432)	5/164	22/268	31/164	35/268	2.251 NS
1992					
Winter (119)	7/43	1/76	4/43	5/76	0.032 NS
Spring (39)	2/19	1/20	3/19	0/20	1.559 NS

Note. For each season, (n) indicate total number of individuals available to move (see text). Movement data from Table 6.5. Classification of the grids is based on their Ivlev's index (Table 6.1). Chi-square tests are comparisons of frequencies of individuals moving - to + and + to - only (1 d.f.).

FIGURE 6.6. Histograms showing the seasonal variation in the frequency of movements of woodmice from grids with low numbers to grids with high numbers (- to +) and vice-versa (+ to -). Grids were classified according to their Ivlev's indices (E_i). Asterisks indicate the significance of X^2 tests comparing the frequency of movements in the two directions; * = $p < 0.05$; ** = $p < 0.01$.

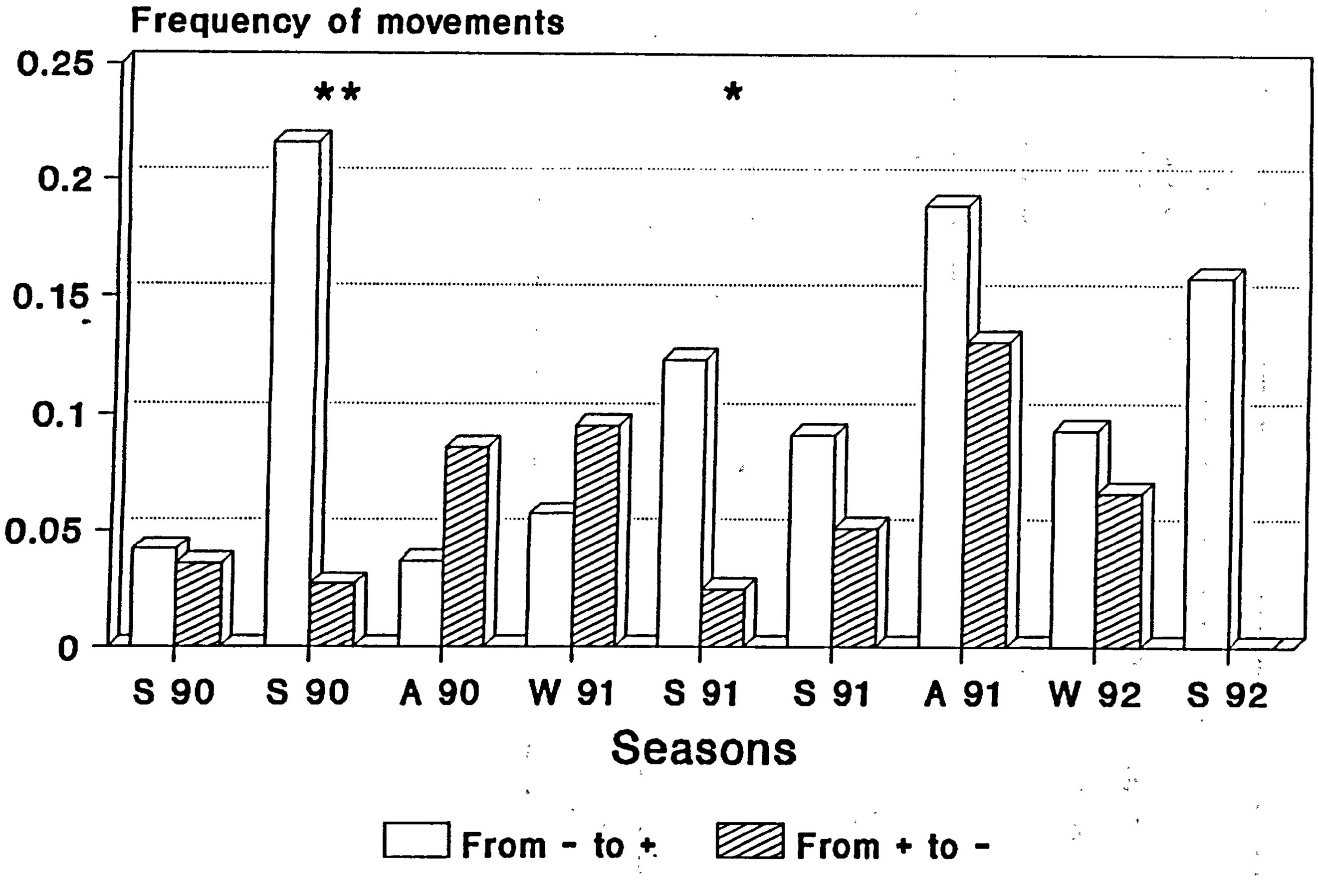


TABLE 6.8. Estimates of 30-day rates of variation in numbers of woodmice (*Apodemus sylvaticus*) caught in each grid within the Corner Complex. Each value expresses variation in numbers (data from Table 5.1) over a period of 30 days, as a proportion of the numbers by the start of the period. Increases and declines in numbers have positive and negative signs respectively. Symbols as in Table 6.1.

Time		Co1(M-F)	Co2(M-F)	Co3(F)	CoS(F)	CoN(M)
1990	May	+ 0.208	- 0.128		-	-
	Jun	-0.600	- 0.273		+ 0.075	- 0.133
	Jul	Felling	Felling		-	-
	Aug	-	-		0.000	+ 0.142
	Sep	+ 1.090	- 0.765	-	0.000	+ 0.500
	Oct	BrashRem	+ 1.860	+ 0.643	+ 6.667	+ 1.444
	Nov	+ *0.369*	- 0.441	+ 0.460	- 0.543	- 0.511
1991	Apr	- *0.606*	- 0.525	- 0.370	+ 1.580	- 1.053
	May	- *0.272*	+ 1.363	+ 0.227	0.000	+ 0.568
	Jun	- *0.343*	+ 0.574	- 0.129	0.000	+ 1.475
	Jul	+ *5.455*	+ 0.779	+ 1.689	+ 1.563	+ 0.091
	Aug	*0*	- 0.052	+ 0.137	+ 0.179	- 0.043
	Sep	- *0.102*	+ 0.057	+ 0.032	+ 0.667	- 0.125
	Oct	+ *2.500*	+ 0.833	BrashRem	+ 0.538	- 0.033
	Nov	- *0.335*	- 0.485	BrashRem	- 0.284	- 0.345
	Dec	- *0.434*	- 0.297	- *0.292*	- 0.310	- 0.500
1992	Feb	- *0.377*	- 0.290	- *0.238*	- 0.305	- 0.293
	Mar	+ *1.070*	- 0.178	+ *2.143*	0.000	0.000

TABLE 6.9. Estimates of 30-day mortality and recruitment rates (i.e mortality and recruitment over a period of 30 days) for *Apodemus sylvaticus* in each grid within the Corner Complex. In each pair of values mortality and recruitment are given by the first and second values respectively.

Time	Co1(M-F)	Co2(M-F)	Co3(F)	CoS(F)	CoN(M)
1990					
May	1.000/0.418	1.000 / 0.448		-/-	-/-
Jun	0.748/0.300	0.858 / 0.682		1.000 / 0.300	0.784 / 0.467
Jul	Felling	Felling			
Aug	-/-	-/-		0.937 / 0.833	0.654 / 1.500
Sep	0.249 / 1.769	0.711 / 0.394	-/-	0.400 / 0.667	0.117 / 0.167
Oct	BrashRem	0.426 / 2.000	0.500 / 0.571	0.500 / 6.333	0.667 / 1.667
Nov	*0.067 / 0.437*	0.823 / 0.294	0.148 / 0.460	0.691 / 0.217	0.718 / 0.170
1991					
Mar	-/-	-/-	-/-	-/-	-/-
Apr	*0.764 / 0.202*	0.497 / 0.000	0.594 / 0.123	0.827 / 1.577	0.469 / 0.000
May	*0.530 / 0.410*	0.000 / 1.360	0.377 / 0.568	0.532 / 0.568	0.265 / 0.908
Jun	*0.201 / 0.343*	0.712 / 0.804	0.129 / 0.259	0.767 / 0.675	0.222 / 1.105
Jul	*0.465 / 2.725*	0.399 / 0.844	0.291 / 1.559	0.313 / 1.875	0.431 / 0.333
Aug	*0.611 / 0.584*	0.394 / 0.420	0.611 / 0.682	0.489 / 0.536	0.392 / 0.392
Sep	*0.329 / 0.255*	0.333 / 0.372	0.313 / 0.260	0.316 / 0.889	0.303 / 0.219
Oct	*0.517 / 2.125*	0.350 / 0.778	BrashRem	0.722 / 1.000	0.403 / 0.163
Nov	*0.619 / 0.201*	0.785 / 0.076	BrashRem	0.685 / 0.133	0.633 / 0.115
Dec	*0.460 / 0.124*	0.442 / 0.093	*0.187 / 0.034*	0.414 / 0.103	0.757 / 0.167
1992					
Feb	*0.692 / 0.000*	0.615 / 0.024	*0.410 / 0.000*	0.408 / 0.017	0.326 / 0.000
Mar	*0.525 / 1.605*	0.695 / 0.357	*0.350 / 2.143*	0.436 / 0.000	0.000 / 0.000

Note. Traces (-) indicate cases where the method does not apply or results are not comparable. Asterisks (*) indicate incomplete grids (during felling). Remaining symbols as in Table 6.1.

TABLE 6.10. Estimates of 30-day emigration and immigration rates (i.e emigration and immigration over a period of 30 days) for *Apodemus sylvaticus* in each grid within the Corner Complex. In each pair of values mortality and recruitment are given by the first and second values respectively.

Time	Co1(M-F)	Co2(M-F)	Co3(F)	CoS(F)	CoN(M)
1990					
May	**0.000 / 0.578**	**0.000 / 0.355**		- / -	- / -
Jun	**0.140 / 0.140**	**0.064 / 0.064**		0.000 / 0.000	**0.000 / 0.000**
Jul	Felling	Felling			
Aug	- / -	- / -		0.000 / 0.000	**0.642 / 0.000**
Sep	0.093 / 0.093	0.125 / 0.000	- / -	0.683 / 0.000	**0.000 / 0.227**
Oct	BrashRem	0.000 / 0.143	0.143 / 0.429	0.000 / 0.333	**0.000 / 0.000**
Nov	*0.000 / 0.557*	0.000 / 0.294	0.153 / 0.153	0.460 / 0.614	**0.000 / 0.080**
1991					
Mar	- / -	- / -	- / -	- / -	- / -
Apr	*0.000 / 0.365*	0.402 / 0.100	0.144 / 0.289	0.000 / 1.303	**0.000 / 0.072**
May	*0.126 / 0.000*	0.417 / 0.627	0.105 / 0.209	0.105 / 0.000	**0.000 / 0.313**
Jun	*0.690 / 0.345*	0.000 / 0.574	0.259 / 0.129	0.000 / 0.000	**0.000 / 0.470**
Jul	*0.680 / 1.365*	0.059 / 0.649	0.130 / 0.390	0.000 / 0.000	**0.029 / 0.323**
Aug	*0.097 / 0.195*	0.157 / 0.472	0.068 / 0.409	0.000 / 0.256	**0.041 / 0.372**
Sep	*0.238 / 0.179*	0.033 / 0.300	0.075 / 0.151	0.046 / 0.092	**0.026 / 0.026**
Oct	*0.000 / 0.385*	0.128 / 0.384	BrashRem	0.000 / 0.462	**0.124 / 0.618**
Nov	*0.033 / 0.067*	0.000 / 0.204	BrashRem	0.049 / 0.268	**0.079 / 0.437**
Dec	*0.062 / 0.558*	0.000 / 0.474	*0.000 / 0.000*	0.188 / 0.047	**0.303 / 0.454**
1992					
Feb	*0.000 / 0.029*	0.000 / 0.072	*0.000 / 0.145*	0.038 / 0.000	**0.036 / 0.072**
Mar	*0.535 / 0.535*	0.000 / 0.535	*0.000 / 0.357*	0.000 / 0.428	**0.000 / 1.070**

TABLE 6.11. Parameters of multiple regression equations relating the variation in number of woodmice in each subpopulation (dependent variable) to mortality, recruitment, emigration and immigration rates at the corresponding grids (independent variables). Separate regressions were calculated for periods of subpopulation increase (top) and subpopulation decline (bottom).

Case (d.f.)	Partial regression coefficients (a ± s.d.) of each independent variable	t of reg. coeffs. and significance (p)	Variance explained by each variable (partial r2)	Variance explained by equation (r2)	Equation's F-value and signif. (p)
dNi,t > 0 (28)	Mortality -0.501 ± 0.195	-2.573 (0.016)	0.197	0.889	53.844 (< 0.001)
	Recruitment 1.132 ± 0.084	13.507 (< 0.001)	0.871		
	Emigration -0 368 ± 0.227	-1.617 (0.118)	0.088		
	Immigration 0.590 ± 0.159	3.705 (< 0.001)	0.337		
	Constant (b) -0.068				
dNi,t < 0 (31)	Mortality -0.676 ± 0.172	-3.936 (< 0.001)	0.341	0.428	5.604 (0.002)
	Recruitment 0.573 ± 0.167	3.425 (0.002)	0.281		
	Emigration -0.459 ± 0.187	-2.451 (0.020)	0.167		
	Immigration 0.235 ± 0.139	-1.693 (0.101)	0.087		
	Constant (b) -0.0408				

6.4 - Discussion

6.4.1 - Habitat selection and population density: contrasting patterns for woodmice and bank voles - For bank voles, the results of both the modified Ivlev's method and the Rosenzweig and Abramsky's method were similar, and they show two points. First, habitat selection in bank voles was strong - much stronger than in woodmice (as shown by the E_O's in Ivlev's method, and by the slope of the regression line in Rosenzweig and Abramsky's). This is consistent with the idea that bank voles have quite marked habitat preferences, due to reasons already discussed in Chapters 3 and 5. The second finding was that in bank voles habitat selection within the Corner Complex was independent of population density.

For woodmice, the two methods gave different results. Ivlev's Ei's showed that woodmice were more widely distributed when numbers are high than when they were low (Figure 6.1), i.e., that habitat selection was density-dependent. This conclusion was confirmed by the results of the regression of E_O on N. However, the results of Rosenzweig and Abramsky's method were inconclusive. None of two hypotheses implying a linear relationship between y' and N* (no habitat selection, or density-independent habitat selection) were supported by the results. It was also not clear whether my results fitted the pattern expected by density-dependent habitat selection, although there was some superficial resemblance (Figure 6.3). Based on the clear results of the modified Ivlev's method, I believe that the most parsimonious hypothesis is that there was density-dependent habitat selection by woodmice in Corner Complex, but Rosenzweig and Abramsky's method neither support nor disprove it.

Habitat selection within Corner Complex thus seemed to be density-independent in bank voles, but density-dependent in woodmice. This result implies that habitat preferences of bank voles were rigid in the sense that no matter how high population densities were, they did not increase their utilization of suboptimal habitats. In contrast, the population of woodmice was quite flexible spatially and when their density was high they readily changed their habitat distribution making heavy use of grids which were underused previously. Besides emphasizing how intense bank voles' habitat preferences are, this contrast between the two species can also be related to the greater vagility of woodmice when compared to bank voles. Among the two species, woodmice have the larger home ranges (Chapter 4) and, even more important, they make long distance movements more often (e.g. Kikkawa, 1964; Bergstedt, 1966; Watts, 1970; Geuse *et al.*, 1985; Harrison, 1990; present study, Section 6.3.2). Woodmice often move distances of several hundred meters under natural conditions (Hacker and Pearson, 1952, Bovet, 1962,

Bergstedt, 1966); during the present study in Hamsterley, two movements longer than 1 km were detected (Appendix 4). All considered, woodmice tend to be less habitat-specialist and more vagile than bank voles. Although there may be other causes involved as well, these two factors surely contribute to the finding that populations of woodmice are spatially fluid and able to respond to changes in population density by expanding their habitat utilization, while bank vole populations do not expand theirs.

6.4.2 - A comment on the methods available to test density-dependent habitat selection - As Rosenzweig and Abramsky's method was proposed by them as a standard technique for the study of habitat selection in small mammals, it is worth investigating its apparent failure in dealing with the data on woodmice in Corner Complex. I propose this was for two reasons, as follows.

(1) The method is based on Simpson's index, which in turn is based on the summation of squared proportions. This tends to under-represent the habitats with the lowest population sizes. For example, two habitats A and B which had respectively 0.5 and 0.1 of the total captures will contribute 0.25 and 0.01 to the summation which gives the value of the index. Thus, grid A had numbers only five times higher than B, but it contributes 25 times more to the index. Therefore, the method is sensitive to variations in preference among the habitats with high numbers, but whether the habitats with low numbers (supposedly the sub-optimal habitats) are little used or not used at all makes little difference. From Table 6.1 it can be seen that variations in numbers among the least-preferred habitats accounts for much of the variation in the overall degree of selectivity, as measured by E_o within the Ivlev's modified method.

(2) The pattern which corresponds to density-dependent habitat selection in a plot of Rosenzweig and Abramsky's y's against N* is not a single linear regression, but three linear functions connected to make a complex function. The method predicts the aproximate shape of this complex function, but does not specify an equation describing it which is amenable to testing. Instead the validity of the prediction is tested by the independent fitting of three linear regressions. There is a considerable degree of subjectivity in deciding which points to include when calculating each of the three linear regressions, which might allow very different patterns to be claimed as confirming the prediction. Thus, the method's ability to falsify the hypothesis of density-dependent habitat selection is smaller than its ability to falsify the alternative hypotheses of no habitat selection or density-independent habitat selection (which can be falsified by data not fitting a single linear regression based on all data points). Cases such as that provided by my

woodmice data, where it is debatable whether the pattern does or does not correspond to the expected density-dependent function, are bound to arise.

Whether the modified Ivlev's method proposed here is reliable to test density-dependent habitat selection in a variety of situations remains to be demonstrated, but the method offers two advantages over Rosenzweig and Abramsky's. First, it provides extra information, i.e., preferences and avoidances of individual grids (E_i). Second, the testing of the hypothesis of density-dependence involves less subjectivity. As a disadvantage, the modified Ivlev's method assumes that the dependence of habitat selection on density is linear along all the range of densities, which may well not be true for many species. It may be possible to expand the method to test alternative models without the linearity assumption, i.e., models where the relationship between E_O and population sizes would be expressed by a single, non-linear equation.

6.4.3 - Density-dependent habitat selection in woodmice: movements or variable local demographies ? - A considerable practical problem in trap-based studies on the role of movements in demographic processes is how to distinguish between true emigration/immigration movements and common within-home-range movements. Any criterion used for this distinction is bound to have shortcomings. For example, using only non-reversed movements would rule out true emigration/immigration movements which are later reversed; this kind of movement is likely to happen in a fluid population using an habitat where the spatial distribution of resources changes temporally. Additionally, some movements between grids within a home range can be perceived as non-reversed emigration/immigration movements because trapping is discontinuous in time. Thus, it is extremely difficult to separate the signal from the noise in this kind of data. Instead of using criteria of dubious value, I did not make any attempt to distinguish immigration/emigration from within-home-range movements, and opted for an alternative approach. I analysed the frequencies of all inter-grid movements, hoping that emigration/immigration fluxes would result in significant differences in the frequencies of movements in two opposite directions. This approach seems to have been successful in some cases, but not in others.

If movements are to explain density-dependent variations in the spatial patterns within Corner Complex as a whole, then one would expect primarily that movements from grids with high numbers to grids with low numbers would be more frequent than vice-versa when population density is high (prediction 1). The complementary phenomenon might also happen: when population densities are low, movements from grids with low

numbers to grids with high numbers could be more common than vice-versa, as individuals seek the best habitats (prediction 2).

In the present study, movements were in the direction expected by prediction 1 during the autumn of 1990 and winter of 1990-91, but in neither case was the difference significant. At similar times in the following year, movements in the direction contrary to the predicted were found slightly more often, but again no significant difference was found.

Prediction 2 was more sucessful than prediction 1. Movements in the predicted direction were more common than vice-versa in all seasons when population densities were low. This difference was significant in summer 1990 and spring 1991, and the difference in frequencies found in spring 1992 could have been significant as well if it had not been for the small sample sizes obtained in that season.

Szacki and Liro (1991) tested what I called prediction 1 for *Apodemus agrarius* and *Clethrionomys glareolus* in a suburban habitat mosaic in Warsaw. In their study prediction 1 applied to some cases, but they also found that "...In many cases directions of movements were not consistent with the density gradient (i.e. more animals moved from less dense into more dense habitats than the opposite direction)" (Szacki and Liro, 1991:222). That is, they found a pattern similar to the one predicted in my prediction 2 as well, but as they were not testing this prediction they did not attribute any meaning to this finding. Unfortunately, as Szacki and Liro did not present their directions of movements separated by season, further comparisons between their results and mine are not feasible.

Overall, from my results on woodmice in the Corner Complex it seems that there was some non-randomness in the direction of movements which was related to the changes in population density of this species. The actual pattern may be sharper than I could detect, as the above mentioned "noise" in these data must have obscured the pattern to some extent.

Supposing that there is indeed pattern in the direction of the movements, the question still remains: how important are they to explain the changes in spatial distribution within the population ?

In the present study, the results of the regression analysis for the increase phase of subpopulations showed two interesting points, as follows. 1) During the increase phase, immigration was of some importance in explaining the growth of subpopulations (although less than recruitment), but emigration was not a significant factor restricting the growth. This pattern suggests that during the increase in subpopulations emigration was less directed than immigration, i.e., emigration rates were not related to variation in grid densities, but immigration was more intense towards the grids where numbers were

increasing most. 2) Whatever the trends in directions of movements, they were less important than differences among local demographies. Recruitment explained more variance in subpopulation sizes than immigration, and mortality more than emigration. It is interesting to note that the most important single factor, juvenile recruitment, reflects to a great extent early juvenile survival, as discussed in Chapter 4.

During the decline phase, the corresponding points were as follows. 1) Emigration was of importance in explaining the decline (although less so than mortality), but immigration was not a significant factor counteracting the decline. Thus, following the same reasoning as in the previous paragraph, it seems that during the decline of subpopulations emigration was more directed than immigration: more individuals left grids where numbers were declining faster, but immigration rates were not related to variations in grid densities. 2) Whatever the trends in emigration/immigration, they were once again less important than local demographies in explaining the population trends.

In summary, immigration contributed significantly to the increase in subpopulations, and emigration contributed to their decline. Such patterns are consistent with the ones expected from the view that what appears to be density-dependent habitat selection is at least partly achieved by non-random movements of individuals among habitats. Nonetheless, the importance of movements was overwhelmed by the importance of local (grid-level) recruitment and mortality.

A word of caution is necessary about the interpretation of these results. The relative importance of local demographies and movements is surely dependent on the spatial scale of the study. This is easily seen by looking at the two extreme hypothetical situations. If grids were too far apart, no intergrid movement would be detected and size of subpopulations would appear to be determined exclusively by local demographies. On the other extreme, if grids were too close to each other, true emigration/immigration movements would be drowned amongst a mass of non-directional home range movements to a extent that all pattern in movements would be obliterated. This second case would lead to an overestimation of the frequency of movements, but to an underestimation of their importance in determining size of subpopulations, as patterns of direction of movements would not be clear-cut. Were movements of paramount importance, probably this could be detected only by studies at an intermediate, optimal spatial scale between the two extremes outlined above. It seems to me (due to the high overall frequency of intergrid movements) that my study design is closer to the second extreme than to the first, and different relative importances of movements and local demographies might be obtained by studies at different spatial scales. As with other parameters in small mammal ecology (population densities, Gurnell and Gipps, 1989; habitat preferences, Morris,

1989), spatial scale influences the measurements obtained, and other comparable studies are necessary to put into context the results of the one described in this Chapter.

CHAPTER 7
GENERAL DISCUSSION

7.1 - Differential responses of woodmice, bank voles and field voles to spatial and temporal habitat heterogeneity. The findings of the present study show that each of the three rodent species responds to spatial and temporal habitat heterogeneity in different ways. To examine these differences further, it is convenient first to make a distinction between field voles on one hand and the woodland rodents (bank voles and woodmice) on the other. As a grassland species, field voles differ from the other two in the way they perceive the habitat mosaic. For woodland species, forests can be seen as "islands" surrounded by a "sea" of unsuitable habitats (Harris 1984, Bauchau and Le Boulengé, 1991). For field voles, young plantations with abundance of grasses are the islands, and the mature forest is the surrounding matrix of unhospitable habitat. This spatial isolation of field vole populations is determined by the temporal isolation of the species within the succession: only the young plantations are a suitable habitat for field voles; the earlier and later successional stages are not (Chapter 3).

In Hamsterley Forest during the present study, most conifer plantations were mature; young plantations and clear-fellings occupied a relatively small area (Figure 2.1). In a forest with this age structure the isolation of field vole populations in space and time would be expected to be particularly marked. Indeed, out of total of 54 standard trapping sessions carried out during the censuses (including S. Gibson's data), field voles were caught during just 11, 10 of which were in young plantations (Chapter 3). At only one site (Road) were field voles always present. Similarly, within Corner Complex, where populations were followed at monthly intervals for two years, field voles were captured in only two out of five grids, and for only short periods of time in both (Chapter 5). Thus in Hamsterley field voles apparently followed and colonized ephemeral suitable habitats, a strategy first proposed for this species by Hansson (1977) and Stenseth (1977). Both these authors regard dispersal as essential for this strategy. However, the comparatively frequent long distance movements required for such dispersal would not be expected in a species whose home range and normal movements are so restricted (Chapter 1). The field evidence of dispersal in field vole populations is discussed below in Section 7.3. As field voles have very restricted habitat preferences it is likely that in this species grassland corridors are important for connecting populations which would otherwise be isolated; habitat corridors are often important to connect small mammal populations in other

fragmented habitats (e.g. Bennett, 1990, Zhang and Usher, 1991). Charles (1981) found that in old conifer stands in Scotland, densities of field voles were much higher in the rides between the mature plantations than in the plantations themselves. In Hamsterley, however, I failed to find evidence of high abundances of field voles in the grassy rides of Corner Complex in 1990 (Chapter 5), but as population densities of this species were very low in the forest as a whole in that year (Chapter 3), my results may reflect the low overall population density rather than inadequacy of the rides as habitat corridors for *M. agrestis* in Hamsterley.

At present, access of field voles to the young plantations I studied should not be a problem because all sites I trapped regularly (except Farm Young) are located along the edges of the forest, adjacent to pastureland and/or to continuous grassy rides bordering main roads. Farm Young is located near pastureland in Pennington Farm and is also bordered by grassy rides along a major road within the forest. As the second rotation continues and more sites are clear-felled and replanted in the central areas of the forest, grassy rides along the internal roads should become increasingly important as habitat corridors for field voles.

Looking further ahead, as the forest goes through further rotations the need for habitat corridors might be reduced again as the proportion of young plantations available within the forest increases, especially in the short rotations used for Sitka spruce. Indeed, a consequence of short rotations is that the age distribution of the plantations in the forest eventually reaches an equilibrium characterized by a high proportion of young stages. A 45-55 years rotation results in an equilibrium proportion of about 40% young plus "closing" plantations; in a 100 year rotation, however, as used in continental Europe, this proportion would be only about 10% (Staines, 1986). Such an increase in the number of suitable patches may help colonization and persistence of local populations by providing "stepping stones" linking the patches (Wilson and Willis, 1975, Shafer 1990), and also by assisting the colonization of the young plantations by suitable grasses. However, my results suggest that, at least in Hamsterley, a future decrease in the importance of the grassy corridors is by no means guaranteed. Several young plantations on the edge of the forest were not used by field voles because of habitat inadequacies, in spite of easy access to such peripherally distributed sites. An increased proportion of young plantations in Hamsterley will make field vole populations less insular only if the soil of most young plantation sites is fertile enough to allow the growth of grasses which are nutritionally and structurally suitable for field voles (Chapter 3).

Among the two rodents lumped together as "woodland" species in the first paragraph of this Section, the responses to habitat fragmentation also differed. I found

woodmice more widely distributed than bank voles on the spatial scales of Hamsterley Forest as a whole and within the Corner Complex. In the forest as a whole, woodmice were captured in 51 out of 54 standard trapping sessions in the censuses but bank voles only in 34 (Chapter 3). Again, on this geographical scale part of the difference between the two species is explained by how frequently they occur along the successional scale. Woodmice were common in all successional stages, but bank voles were seldom abundant in clear-fellings, with the exception of the site Corner 2 in 1992 (Chapter 3). Another part of the difference resulted from the more restricted habitat preferences of bank voles than woodmice within the young plantation stage (Chapter 3), chiefly a result of the former species' greater dependence on ground cover, as discussed in Chapters 1 and 3 and shown experimentally in Chapter 5.

At the smaller spatial scale, within Corner Complex, the same pattern of differential responses of woodmice and bank voles to temporal heterogeneity was observed. Woodmice were seldom absent, from any site at any time, while bank voles were absent from one or more sites during most of the study (Chapter 5). Wood mouse populations were also more equitably distributed among sites, as shown by their indices of overall degree of habitat selection, E_0's (Chapter 6). This pattern seems to be related not only to the wider habitat preferences of woodmice, but also to their greater vagility. Within Corner Complex, woodmice had larger home ranges than bank voles (Chapter 4) and moved between sites significantly more often (Chapter 6). Additionally, the vagility of woodmice was illustrated by the two long distance movements discussed in Appendix 4. In turn, the differences in habitat preferences and vagility are related to the other ecological differences between the two species discussed in Chapter 1. For example, woodmice are relatively more vagile because their food is sparsely distributed, and also because they depend little on ground cover for anti-predator defence. All these aspects of their ecology interact with each other and constrain each other, forming an "adaptive suite" (*sensu* Bartholomew, 1972, quoted in Pianka, 1988). The differences between their respective adaptive suites determine different and to a certain extent predictable responses of woodmice and bank voles to spatial and temporal habitat heterogeneity.

If this view is correct, the characteristic responses of these two species to spatial heterogeneity should be similar in a wide variety of situations. In fragmented deciduous woodland in Belgium, local extinctions and recolonizations were common for bank voles, but not for woodmice; this result was attributed to woodmice having wider habitat preferences and moving longer distances than bank voles (Geuse *et al.*, 1985; Bauchau and Le Boulengé, 1991). Dickman and Doncaster (1987, 1989) found that bank voles were absent from individual patches significantly more often than woodmice in an urban

habitat mosaic in Oxford. All these findings are similar to my findings in Hamsterley. On the other hand, Dickman and Doncaster (1989) and Szacki and Liro (1991) did not find a significant difference in the frequency of long movements by the two species in urban habitat mosaics, neither did Zhang and Usher (1991) in an agricultural landscape in Yorkshire. In my opinion, the most common pattern of responses of these two species to spatial heterogeneity (at least in mosaics with discontinous cover) is probably the one found in Belgium and in Hamsterley: namely, that bank vole populations are more patchily distributed and more isolated from each other than wood mouse populations. However, even though these two rodent species are so well studied, it is not yet established how general this distributional pattern is, and some open questions remain, especially concerning movements. We need better knowledge of the maximum distances moved by these species, how frequent are long distance movements, and what proportion of animals undertaking them return at a later date. Only when such questions are answered satisfactorily in a variety of habitats we will be able to improve our ability to generalize as to how these species cope with habitat fragmentation.

7.2 - A possible role of mature Sitka spruce in increasing spatial heterogeneity in the young plantations - As discussed in Chapter 1, Sitka spruce probably impoverishes the soils on which it is planted, particularly by acidification and podzolization, although the extent of the impoverishment is still debatable. In the present study, I found that rodent communities were most variable in young plantations by comparison with other stages of Sitka spruce succession; this variation was associated with local differences in ground vegetation which in turn were associated with high local variation in soil types (Chapter 3). Some of the local soil variation within Hamsterley Forest surely pre-dates the planting of Sitka spruce there and other plant species (e.g., heather) may also contribute to soil acidification (Miles, 1986). However, many of the differences I found between soils were due either to different degrees of podzolization (going from typical gleys through podzolic gleys to typical podzols) and some were due to poor decomposition of organic matter under very acidic conditions; both these effects can be attributed, at least partly, to Sitka spruce (Miles, 1986). More important, soils under Sitka in different localities can suffer acidification and podzolization to different degrees according to date of planting, density of planting, length of rotation, in addition to the local variations in the susceptibility of the soil to impoverishment (Chapter 1). Thus it is likely that planting of areas with Sitka spruce can increase spatial variation of soils, that is, soil heterogeneity is to some extent a product of soils at different sites being modified by Sitka to different degrees. If this is correct, we have the paradox that the relatively homogeneous mature forest where local

variation is "buffered" (Chapter 3) contributes to the considerable heterogeneity of both ground vegetation and rodent communities in the young plantations that will follow it.

An extension of this view is that local variation in rodent communities would increase during the first few rotations (at least from first to second), but decrease again thereafter as all soils within the forest become equally poor. This view is dependent on the assumption that planting of Sitka results in a progressive long-term impoverishment of soils. The data available so far on long-term impacts of conifers on soils are not enough to decide whether this assumption is valid or not (Miles, 1986).

7.3 - Flexibility in habitat preferences and population regulation - As emphasized by Montgomery (1989a, 1989b) there are two kinds of density-dependence which can play a part in population regulation: temporal density-dependence and spatial density-dependence. Temporal density-dependence, i.e., density-dependence in the time-series of abundances, is well established as one important factor in the regulation of wood mouse populations (Watts, 1969, Flowerdew, 1985, Montgomery, 1989a; see Chapter 4). Spatial density-dependence, i.e. density-dependent habitat selection, has been shown only recently for *A. sylvaticus* by Montgomery (1989b, 1989c) in two studies in, respectively, conifer plantations in Northern Ireland and mixed deciduous woodland in southwest England. In the second study, woodmice showed a tendency to expand their use of suboptimal habitats when density of conspecifics was high, but the contrary happened when a superior competitor (the yellow-necked mouse, *A. flavicollis*) was present at high densities. In Hamsterley, where *A. flavicollis* is absent, habitat selection by *A sylvaticus* was more clearly dependent on its own density (Chapter 6).

The interaction between the two forms of density-dependence has seldom been studied in small mammals, but this is a promising avenue of research, especially in relation to population regulation. Fascinating hypotheses can be developed and tested. For example, it is known that some simple mathematical models describing population variation, based on non-linear difference equations, show a surprisingly rich array of dynamic behaviour (May, 1976). A single model can produce either stable populations, regular annual fluctuations, two or four (or more) year regular cycles, or non-cyclic, "chaotic" variation, as the value of a single parameter - r, the intrinsic rate of population growth - increases above successive thresholds (May, 1976; May and Oster, 1976). There is some terminological confusion about r, I use it here to mean the rate at which the population would grow, at a given locality and time, in the absence of density-dependent effects restricting the growth. This definition is consistent with the most usual meaning of r (Begon and Mortimer, 1986: 47). In mathematical terms, the parameter r determines the

degree of non-linearity of the population growth. May and Oster's original models applied to populations showing reproductive and non-reproductive periods, and non-overlapping generations. The first condition applies to rodents living at high latitudes, the second not; but slightly more complex models with behaviour similar to the ones described by May and Oster can be obtained assuming overlapping generations as well. An interesting feature of such models is that a single species may show either regular annual fluctuations, or regular pluriannual cycles, or non-cyclic pluriannual variations, without the need to invoke extensive changes in its population processes: which mathematical behaviour the population shows depends only on the value assumed by r. This means that there may not be a specific cause for cyclicity, as cyclicity in itself need not be an event requiring a specific explanation, but only one behaviour within a continuum of possible behaviours expected from a single model.

If the view expressed above is true, it should be possible to find examples of single microtine populations showing completely different dynamic behaviours at different times even in the absence of any obvious changes (either in habitat or intrinsic to the population) which could be associated with a change in the regulatory mechanisms of the population There are several published studies which seem to show examples of this. Such variety of dynamic behaviour in a single population has been found by Getz *et al.* (1987) who studied populations of *Microtus ochrogaster* and *M. pennsylvanicus* in grasslands in Illinois, U.S.A. for fourteen years; their results are clearly consistent with the view expressed above. Southern and Lowe (1982) and Taitt and Krebs (1985, quoted in Lidicker, 1988) provide additional examples of a single microtine population showing either annual fluctuations or pluriannual cycles at different times. It is well established that there are several marked demographic changes (in survival rates, recruitment rates and spatial patterns) during population cycles, as reviewed, for example, by Myllymaki (1977b) for *Microtus agrestis*. However, many of these changes could be effects of the drastic changes in density during cycles, rather than a primary cause of the cyclicity itself, which would be a result of the same population mechanisms found in the non-cyclic populations, only with a different value for the parameter r.

Thus, the question would reduce to: for a particular species, what makes the parameter r - i.e. the rate at which the population would grow in the absence of density-dependent effects - vary between different localities, or at different times in the same locality ? While variations in r as a result of changes in the environmental conditions are to be expected (Flowerdew, 1987: 115), to determine the causes of the variation in r in natural conditions is not a simple question, because this parameter represents a composite of a series of factors influencing population growth through their effects on birth and

death rates (Begon and Mortimer, 1986). Thus, even if cyclicity and non-cyclicity are different behaviours shown by a single model, which behaviour the population shows could be influenced by a variety of causal factors - as in the multifactorial view that W. Lidicker has advocated with a regular five-year cyclicity (Lidicker, 1973, 1978, 1983, 1988).

I propose, as an hypothesis, that density-dependence in habitat selection could be one of these factors, because by definition density-dependent effects will be triggered by an increase in population density (numbers per unit area) rather than in population size itself. A given r would result in a much lower increase in population density if, when numbers increase, the population is spread over a larger area. This would be equivalent to a lower value of r, if considered in relation to the numbers present only in the original area of distribution.

If a population of a density-dependent habitat selector starts to grow quickly in the optimal habitat, the increase in population density in this habitat is restrained by increasing the use of suboptimal habitats, and as a result r never exceeds the threshold value that would make the population become cyclic. If on the other hand the species is a density-independent habitat selector, it does not use the "escape valve" of suboptimal habitats, and the increase in density in the preferred habitat is not restrained: r may go above the threshold and the population may become cyclic.

This hypothesis is analogous to the "social fence" hypothesis proposed by Hestbeck (1982), but with a difference. Hestbeck suggested that, during a population "cycle", at low population density only the optimal habitat is occupied, but when the population grows surplus individuals disperse into suboptimal habitats around the original (optimal) habitat. Dispersal continues until all vacant spaces are filled in the suboptimal habitats. Once such population density has been reached, the spacing behaviour of the individuals in the suboptimal habitats would "fence" the central population, preventing further dispersal. This would cause the population in the optimal habitat to be "regulated by resource exhaustion" resulting in cyclical pluriannual fluctuations (Hestbeck, 1982). I suggest that for some populations habitats other than the optimal might simply not be occupied, because the population shows density-independent habitat selection. The "fence" imprisoning the population would not be a social one, but simply the rigidity of its own habitat preferences.

Several other recent models (see Hansson and Stenseth, 1988) have also analysed the relationship between spatial heterogeneity and population cyclicity in microtine rodents. Such models were reviewed by Gliwicz (1988) who pointed out that different models have led to contradictory conclusions, some finding that cyclicity should require

habitat heterogeneity, and some finding that cyclic populations should occur in more homogeneous habitats. The hypothesis I suggest here is not based on spatial heterogeneity alone; it is based also on the different extents to which each local population changes its use of space in response to variations in population density. These differences depend not only on the spatial heterogeneity found at a given place and time but also on how the peculiarities of the biology of each species affect its response to such spatial heterogeneity, as discussed in Chapter 6 and in Section 7.1.

If we accept that some of the factors which influence r vary latitudinally (e.g., length of breeding season and intensity of breeding), the hypothesis I suggest is consistent with bank voles and field voles being cyclic at higher latitudes but not at lower latitudes. Any hypothesis on the causes of cyclicity should be able to explain such intraspecific gradients of cyclicity (Hansson and Henttonen, 1985, Stenseth, 1985). Looking at the most common small British rodents, woodmice are never cyclic across their range in Europe, bank voles are sometimes cyclic and sometimes not, and field voles are cyclic in most areas. The few studies of density-dependent habitat selection made so far suggest that woodmice are density-dependent habitat selectors, and bank voles were found to be density-independent habitat selectors in the present study (Chapter 6). A testable prediction of my hypothesis is that field voles should be density-independent habitat selectors, at least in most cases.

As yet it is not clear whether this last point is true or not, as to my knowledge there is no published study analysing specifically density-dependence in habitat selection in *Microtus agrestis*. As their habitat preferences are even more restricted than bank voles' (Chapter 1), I would expect field voles to be density-independent habitat selectors, especially in habitats such as conifer plantations, where sites are either favourable or clearly unfavourable (Chapter 3). On the other hand, several demographic models proposed for field voles assume that they are actually density-dependent habitat selectors. Such models have attributed an important role to dispersal to suboptimal habitats during the increase phase of population cycles (e.g. Hansson, 1977, 1989, Stenseth, 1977, 1980, 1985, Stenseth *et al.*, 1977, Hestbeck, 1982), but the strength of the field evidence on the actual importance of dispersal, especially in cyclic populations, seems questionable. For example, in their recent review Gipps and Alibhai (1991) quote the studies by Hansson (1977), Myllymaki (1977c) and Viitala (1977) to indicate the extent of dispersal in *M. agrestis*. All these three studies provide only incidental evidence of a few dispersive events; none of them quantifies dispersal rates (either frequency of movements per unit of time, or as a proportion of the population size). The occurrence of some density-dependent dispersal, in itself, does not necessarily mean that its intensity is enough to

regulate the population through a substantial rearrangement in the spatial distribution. There is some evidence that in Fennoscandia field voles use some suboptimal habitats when population densities are high (e.g. Hansson, 1977, Erlinge *et al.*, 1983), but their numbers in such habitats are usually low. Additionally, Stenseth recognizes that cyclicity is more likely in homogeneous habitats, where there are less opportunities for dispersal. Thus, in my opinion there is no conclusive evidence yet of marked density-dependence in habitat selection in most field vole populations.

If field voles are found to be density-independent habitat selectors, then among woodmice, bank voles and field voles there would be an inverse relationship between the degree of flexibility in habitat selection and frequency of population cyclicity. This relationship would be consistent with the hypothesis I propose, although it would not, of course, prove it. Furthermore, I would expect density-dependent habitat selection to be only one of several factors influencing cyclicity, as there are several factors which affect the value of the parameter r (see above).

I suggest that the hypothesis I present here is worth testing, which could be achieved by comparing density-dependence in habitat selection in cyclic and non-cyclic small mammal populations in heterogeneous habitats. Regardless of whether this particular hypothesis is true or not, it seems clear that an understanding of small mammals' responses to spatial heterogeneity can help us to understand better their responses to temporal heterogeneity, one of the oldest problems of ecology.

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APPENDIX 1 - PROGRAM AGECLASS

Ageclass is a SAS program, written by E. Le Boulengé and me, to allocate individuals irreversibly to age classes by body weight (see text, Section 4.2.2),

```
1          /*********** SAS procedure to create an ageclass (Agecl) based upon
2          /*********** the value of Weight (according to species)
3          /*********** and with non-decreasing value - It replaces weiclas
4          cms filedef in disk f$indiv data a;
5          cms filedef sortie pun;

6          Data capt;
7            infile in;
8            input grid $ agegrid $ species $ tag $
9                  sex $ date line column weight rep $ alive $ taglos $
10                 ntag $ weiclas $ glin  gcol weicl session;
11
12         /*  ----Sorting file by Individual and Capture Date---------- */

NOTE: The infile IN is:
      Filename=F$INDIV  DATA     A1,
      Recfm=FB  ,Lrecl=60,Blksize=1020

NOTE: 3058 records were read from the infile IN.
NOTE: The data set WORK.CAPT has 3058 observations and 18 variables.

13         PROC SORT;
14          BY TAG DATE;
15
16         /*  ----Calculating Date of first capture of Individuals--------- */
17         /*  ----- and calculating the value of Agecl (not decreasing) ---- */

NOTE: SAS sort was used.
NOTE: The data set WORK.CAPT has 3058 observations and 18 variables.

18         DATA; SET; BY TAG DATE;
19          RETAIN PREM 0 ageclant 0;
20             if weight = . | weight = 0 then agecl = 0;
21             else if weight < 16 then agecl = 1;
22                  else if species='CG' then do;
23                          if weight < 20 then agecl=2;
24                                         else agecl=3;
25                  end;
26                  else do;
27                          if weight < 21 then agecl=2;
28                                         else agecl=3;
29                  end;
30         IF FIRST.TAG THEN  PREM=DATE;
31            else if agecl<ageclant then agecl = ageclant;
32                                   else;
33         ageclant=agecl;
34
```

```
35          Proc sort;
36            by prem tag date; /* ----- Reorder the file ----------------*/
37

NOTE: SAS sort was used.
NOTE: The data set WORK.DATA1 has 3058 observations and 21 variables.

38          Proc format;
39           /* --------- Produce labels for the values of Agecl ---------- */
40            value AGEFMT
41              0 = '?'
42              1 = 'j'
43              2 = 's'
44              3 = 'A';
NOTE: Format AGEFMT has been output.


45          Data; Set;
46            file sortie;
47            PUT grid $CHAR3. @5  agegrid $CHAR1. @7 species $CHAR2. @10 tag
48          $CHAR3. @14 sex $CHAR1. @16 date 3. @20 line 2. @23 column 2. @26
49                weight 2. @29 rep $CHAR1. @31 alive $CHAR1. @33 taglos $CHAR4.
50                  @38 ntag $CHAR5. @45 agecl AGEFMT1. @47 glin 2. @50 gcol 2.
51                  @53 weicl 1. @55 session 2.;

NOTE: The file SORTIE is:
      Filename=PUNCH                    ,
      Recfm=F    ,Lrecl=80,Blksize=80
```

APPENDIX 2 - PROGRAM FCOORD

Fcoord is a SAS program, written by E. Le Boulengé and me, to translate capture locations (grid number and trap number) into locations in a common system of spatial coordinates, based on the actual distances and angles between the grids.

```
1          /************ SAS procedure to calculate "pooled" trap coordinates
2          cms filedef in disk f$indiv data a;
3          cms filedef sortie pun;

4          Data capt;
5            infile in;
6            file sortie;
7            input grid $ agegrid $ species $ tag $
8                  sex $ date line column weight rep $ alive $ taglos $
9                  ntag $ waiclas $ glin  gcol session;
10
11           if grid='BLC' and line <3 then do;
12             alpha=32; x=column; y=line; dx=0.666667; dy=dx;
13             if line=1 then do; x0=5; y0=81; end;
14                       else do; x0=8; y0=86; y=y-1; end;
15             end;
16           else if grid='COX' then do;
17             alpha=32; x=column; y=line; dx=-1; dy=1; x0=42; y0=102;
18           end;
19
20           else if grid='CO2' then do;
21             alpha=35;
22             if agegrid='X' then do;
23               x=column; y=line; dx=0.666667; dy=-dx; x0=38; y0=91;
24             end;
25             else do;
26               x=line; y=column; dx=-1; dy=dx; x0=45; y0=95;
27             end;
28           end;
29
30           else if grid='CO1' then do;
31             alpha=18;
32             if agegrid='X' then do;
33               x=column; y=line; dx=0.666667; dy=-1; x0=33; y0=44;
34             end;
35             else do;
36               x=line; y=column; dx=1; dy=dx; x0=36; y0=34;
37             end;
38           end;
39
40           else if grid='CO3' then do;
41             alpha=23; x=column; y=line; dx=1; dy=dx; x0=62; y0=39;
42           end;
43
44           else if grid='COS' then do;
45             alpha=33; x=line; y=column; dx=1; dy=-1; x0=51; y0=20;
46           end;
47
48           else x=.;
49
```

```
50          if x ne . then do;
51            x = x-1;  y = y-1;                    /* Distance to origin of grid */
52            alpha=alpha * 3.14159 / 180;          /* Alpha in radians */
53            R11 = cos(alpha); R22 = R11;          /* Rotation matrix  */
54            R21 = sin(alpha); R12 = -R21;
55            x0=x0 / 3;                            /* Origin of grid in 15m units */
56            y0=y0 / 3;
57            NewX = x0 + R11 * x * dx + R12 * y * dy;
58            NewY = y0 + R21 * x * dx + R22 * y * dy;
59              NewX = round(NewX) + 1;
60              NewY = round(NewY) + 1;
61          end;
62          else do; NewX=.; NewY=NewX; end;
63
64          PUT grid $CHAR3. @5  agegrid $CHAR1. @7 species $CHAR2. @10 tag
65        $CHAR3. @14 sex $CHAR1. @16 date 3. @20 line 2. @23 column 2. @26
66              weight 2. @29 rep $char1. @31 alive $char1. @33 taglos $char4.
67                @38 ntag $char5. @45 weiclas $char1. @47 NewY 2. @50 NewX 2.
68                @53 session 2.;

NOTE: The infile IN is:
      Filename=F$INDIV  DATA     A1,
      Recfm=FB  ,Lrecl=80,Blksize=960

NOTE: The file SORTIE is:
      Filename=PUNCH                ,
      Recfm=F    ,Lrecl=80,Blksize=80
```

APPENDIX 3

CORRECTING POPULATION SIZE ESTIMATES FOR THE VARYING NUMBER OF GRIDS: EFFECTS ON THE CORRELATIONS BETWEEN POPULATION SIZES AND OTHER PARAMETERS

TABLE APPENDIX 3. Pearson's correlation coefficients between population size (as estimated by the Manly-Parr method) and other demographic and spatial parameters, comparing population size estimates corrected for the number of grids actually trapped, and uncorrected estimates (see text, Section 4.2.2).

Comparison	d.f.	Uncorrected		Corrected	
		r	p	r	p
a) Demographic rates correlated with N_t					
Total survival, As	16	0.2520	> 0.20	0.0800	> 0.50
Total survival, Cg	15	0.2676	> 0.20	0.0943	> 0.50
Adult survival, As	17	0.3374	0.05 < p < 0.10	0.2271	> 0.10
Adult survival, Cg	17	0.6347	< 0.01 **	0.6056	< 0.01 **
Subadult survival, As	17	-0.0179	> 0.50	-0.1495	> 0.25
Subadult survival, Cg	17	-0.0201	> 0.50	0.0978	> 0.50
Juvenile survival, As	16	0.1972	> 0.10	0.0307	> 0.50
Juvenile survival, Cg	14	0.3675	0.05 < p < 0.10	0.1113	> 0.25
Juvenile recruitment, As	17	0.6404	< 0.01 **	0.5788	< 0.01 **
Juvenile recruitment, Cg	17	0.4208	< 0.05 *	0.4653	< 0.05 *
Prop. reprod. females, As	17	-0.0630	> 0.50	-0.1232	> 0.25
Prop. reprod. females, Cg	17	-0.4191	< 0.05 *	-0.5153	< 0.05 *

(to be continued - see next page)

Table Appendix 3 (continuation)

b) Demographic rates correlated with Nt - 1	d.f.	Uncorrected		Corrected	
		r	p	r	p
Total survival, As	15	-0.5911	< 0.01 **	-0.4496	< 0.05 *
Total survival, Cg	14	0.1678	> 0.25	0.1010	> 0.50
Adult survival, As	16	-0.2472	> 0.20	-0.3416	0.05 < p < 0.10
Adult survival, Cg	16	0.4782	< 0.05 *	0.4282	< 0.05 *
Subadult survival, As	16	-0.0252	> 0.50	-0.0372	> 0.50
Subadult survival, Cg	16	0.0157	> 0.50	0.0442	> 0.50
Juvenile survival, As	15	-0.1432	> 0.25	-0.1732	> 0.25
Juvenile survival, Cg	14	0.3870	0.05 < p < 0.10	0.2501	> 0.10
Juvenile recruitment, As	16	0.4117	0.05 < p < 0.10	0.3386	0.05 < p < 0.10
Juvenile recruitment, Cg	16	0.0598	> 0.50	0.0708	> 0.50
Prop. reprod. females, As	16	-0.5830	< 0.01 **	-0.6248	< 0.01 **
Prop. reprod. females, Cg	16	-0.7071	< 0.01 **	-0.7613	< 0.01 **
c) Home ranges / distances moved (DMs) x seasonal N					
Male home ranges, As	8	-0.7058	< 0.05 *	-0.6991	< 0.05 *
Male home ranges, Cg	5	0.1236	> 0.50	0.0505	> 0.50
Female home ranges, As	8	0.0872	> 0.50	0.0866	> 0.50
Female home ranges, Cg	6	0.4804	> 0.10	0.6510	> 0.10
Male DMs, As	8	-0.5734	0.05 < p < 0.10	-0.6120	0.05 < p < 0.10
Male DMs, Cg	7	-0.7236	< 0.05 *	-0.7498	< 0.05 *
Female DMs, As	8	0.2346	> 0.25	0.1706	> 0.25
Female DMs, Cg	8	0.4372	> 0.10	0.4903	> 0.10
d) Regressions, Ivlev's modified method's E_0 x N		F		F	
E_0 x N, As	17	5.1650	< 0.05 *	7.0180	< 0.05 *
E_0 x N, Cg	17	3.3210	0.05 < p < 0.10	2.3940	> 0.10

Note. Symbols: As, *Apodemus sylvaticus*; Cg, *Clethrionomys glareolus*; d.f., degrees of freedom; r, correlation coefficient; F, Fisher's ratio; p, one-tail probability of each value of r and F; asterisks (*) indicate significant results: * = $p < 0.05$ and ** = $p < 0.01$.

APPENDIX 4
SOME LONG DISTANCE MOVEMENTS OF WOODMICE

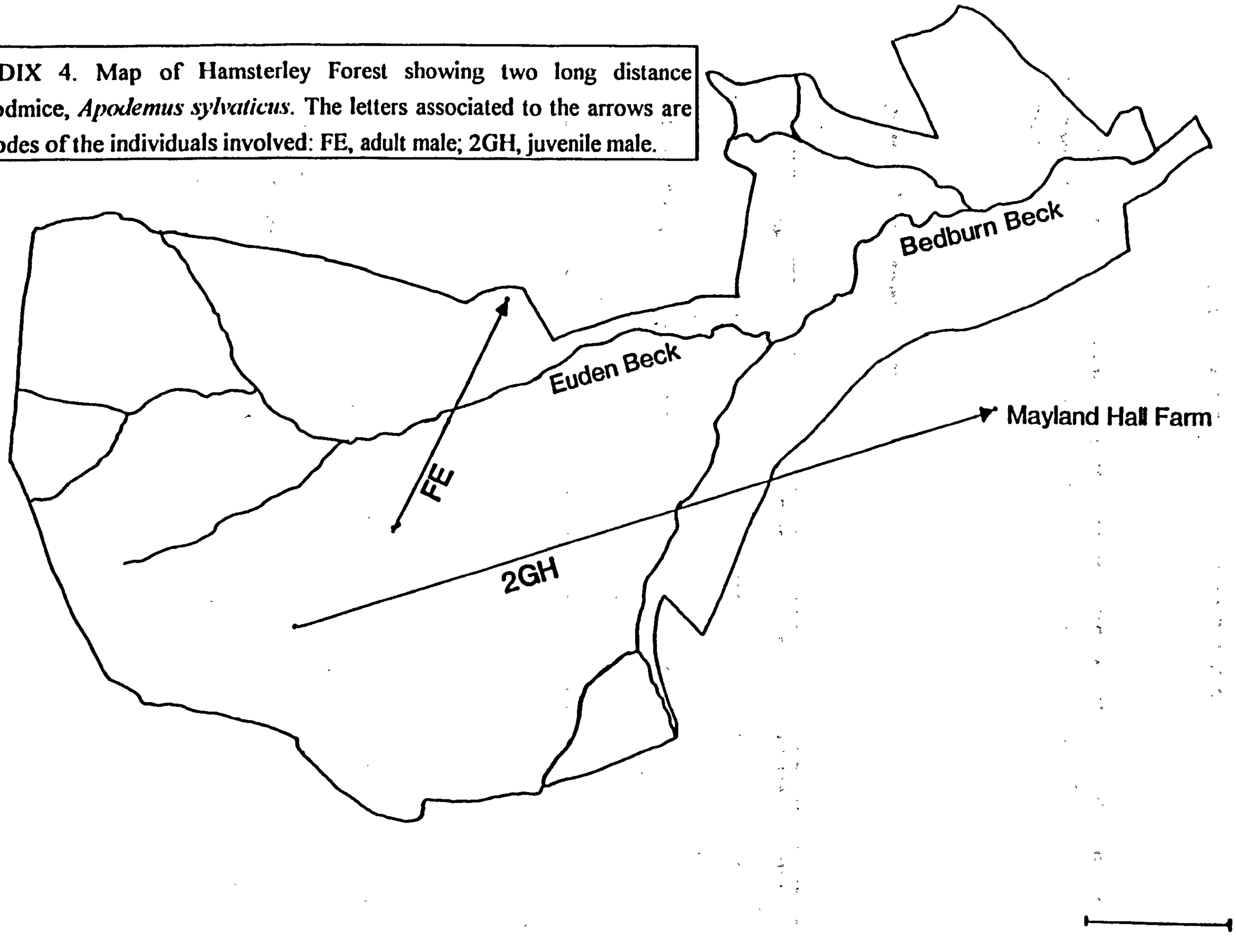
While many ecologists believe that long distance movements (i.e. longer than 1 Km) are common in woodmice (W.I. Montgomery, pers. comm.), there seems to be little published field evidence proving this point. During the present study in Hamsterley Forest, two exceptionally long movements were detected. These movements were longer than any natural movement previously recorded for *Apodemus sylvaticus* (compare, for example, with Bovet, 1962, Kikkawa, 1964, Bergstedt, 1966, Watts, 1970, Geuse *et al.*, 1985, Wolton and Flowerdew, 1985); they exceed even the 1.5 Km recently recorded by Szacki and Liro (1991) for the congeneric species *A. agrarius*. The characteristics of the two movements I recorded were as follows.

1) Movement by a fully reproductive adult male, weighing 22 g. After being captured twice in a young Sitka spruce plantation (grid Corner East) on 18 and 20 June 1990, it was next captured three weeks later (11 July) in a clear-felling in the North of the forest (grid View). The straight line distance between the two points is 1,750 m (as estimated, to the nearest 50 m, by plotting the displacement on a map of scale 1:10,000); the two sites are separated by a stream, Euden Beck (Figure Appendix 4). After this movement, it was recaptured twice in View, on the two following days, before disappearing from the population.

2) Movement by a non-reproductive juvenile male, weighing 14 g (before the movement). It was captured three times in October 1991 (the last on 17) in the grid Corner South, a clear-felling. It was next found thirty-six days later (22 November), killed by a breakback trap set near the buildings of Mayland Hall Farm. Such buildings are surrounded by improved pastureland, and located 5,100 m away in straight line from the original capture point, also across a stream, Bedburn Beck (Figure Appendix 4).

The distances quoted should be regarded as minimum estimates of the actual distances travelled, because they were measured in a straight line and it is most unlikely that the animals themselves followed such a route, as they had to cross streams. Judging by their distances alone, the two displacements I detected were probably dispersive movements. These findings show that *Apodemus sylvaticus* is capable of making very long movements in nature. Although this is not unexpected in view of the high vagility of this rodent both within its home range (e.g. Wolton, 1985; Attuquayefio *et al.*, 1986) and during dispersal (see references quoted above), the present note is the first case, to my knowledge, in which natural movements of such a length were actually recorded for this species.

FIGURE APPENDIX 4. Map of Hamsterley Forest showing two long distance movements of woodmice, *Apodemus sylvaticus*. The letters associated to the arrows are the identification codes of the individuals involved: FE, adult male; 2GH, juvenile male.



APPENDIX 5
DATES OF THE TRAPPING SESSIONS

The dates listed below refer to standard four-day trapping sessions, as described in Chapter two; traps were placed in the first day and checked in the three following days.

a) Dates of the censuses (Chapter 3)

Successional stages	Site	Winter 1990	Summer 1990	Summer 1991	Summer 1992
Clear-fellings	Farm Felled	20-23/02	02-05/07	09-12/07	15-18/06
	View	05-08/03	11-14/07	10-13/07	16-19/06
	Corner South		25-28/06	27-30/06	08-11/06
	Corner 2			21-24/06	09-12/06
	Corner East		18-21/06		
	Corner 3			20-23/06	
Young (5-8 yrs old)	Hut	06-09/03	25-28/06		
	Adder	05-08/02	12-15/06	12-15/07	02-05/06
	Farm	19-22/02	02-05/07	10-13/06	15-18/06
	Scots Pine	06-09/03	02-05/07	09-12/07	02-05/07
	Road		10-13/07	12/15/07	02-05/07
	Stuart		02-05/07	10-13/07	01-04/07
	Corner Young		18-21/06		
Mature (about 40 yrs old or more)	Adder Mature	06-09/02			
	Corner 1	28-31/03	18-21/06		
	Corner 2	28/31/03	18-21/06		
	Hut Mature		25-28/06		
	Corner North		12-15/07	27-30/06	02-05/07
	Farm Mature		02-05/07	10-13/06	15-18/06

APPENDIX 5 (cont.)

b) Dates of trapping of the population study in Corner Complex (Chapters 4 to 6). Symbols as in Table 5.1, Chapter 5.

Month		Co1(M-F)	Co2(M-F)	Co3(F)	CoS(F)	CoN(M)
	Mar	28-31	28-31	-	-	-
	Apr	23-26	23-26	-	-	-
	May	28-31	28-31	-	07-10	07-10
	Jun	18-21	18-21	-	25-28	25-28
1990	Jul	Felling	Felling	-	28-31	12-15
	Aug	15-18	15-18	-	14-17	14-17
	Sep	26-29	25-28	25-28	26-29	26-29
	Oct	BrashRem	28-31	28-31	26-29	26-29
	Nov	14-17	12-15	12-15	19-22	20-23
	Dec	03-06	04-07	03-06	-	-
	Feb	25-28	25-28	25-28	-	-
	Mar	12-15	12-15	12-15	19-22	19-22
	Apr	08-11	08-11	08-11	09-12	09-12
	May	21-24	21-24	21-24	22-25	21-24
1991	Jun	20-23	21-24	20-23	27-30	27-30
	Jul	22-25	23-26	22-25	28-31	28-31
	Aug	13-16	13-16	13-16	19-22	19-22
	Sep	24-27	25-28	24-27	17-20	17-20
	Oct	14-17	14-17	BrashRem	16-19	22-25
	Nov	11-14	11-14	BrashRem	19-22	19-22
	Dec	03-06	03-06	09-12	09-12	09-12
	Feb	10-13	10-13	11-14	24-27	24-27
1992	Mar	09-12	09-12	09-12	16-19	16-19
	Jun	08-11	08-11	08-11	09-12	16-19